Les microhabitats des arbres : facteurs d'influence, lien avec la biodiversité et potentiel indicateur

Yoan Paillet

MUSEUM NATIONAL D'HISTOIRE NATURELLE

Ecole Doctorale Sciences de la Nature et de l'Homme – ED 227

Année 2018 **N°attribué par la bibliothèque**
|_|_|_|_|_|_|_|_|_|_|_|_|_|

THESE

Pour obtenir le grade de

DOCTEUR DU MUSEUM NATIONAL D'HISTOIRE NATURELLE

Spécialité : Ecologie

Présentée et soutenue publiquement par

Yoan Paillet

Le 20 septembre 2018

Les microhabitats des arbres : facteurs d'influence, lien avec la biodiversité et potentiel indicateur

Sous la direction de :

Monsieur Guilbert, Eric, Maitre de Conférence (HDR), UMR 7179 MECADEV

Monsieur Archaux, Frédéric, UR EFNO, Irstea

JURY :

Mme Jane, Lecomte	**Professeure, ESE, Université Paris-Sud, Orsay (091)**	**Présidente**
M. Guilbert, Eric	**Maitre de Conférences (HDR), UMR 7179 MECADEV, Paris (075)**	**Directeur de Thèse**
M. Besnard, Aurélien	**Maitre de Conférence (HDR), UMR 5175 CEFE, Montpellier (034)**	**Rapporteur**
M. Jactel, Hervé	**Directeur de Recherche, UMR 1202 BIOGECO INRA, Cestas (033)**	**Rapporteur**
Mme Andrieu, Emilie	**Chargée de Recherche, UMR 7204 Dynafor INRA, Castanet-Tolosan (031)**	**Examinatrice**
M. Julliard, Romain	**Directeur de Recherche, Muséum national d'histoire naturelle, Paris (075)**	**Examinateur**
M. Archaux, Frédéric	**Ingénieur-Chercheur, UR EFNO Irstea, Nogent-sur-Vernisson (045)**	**Invité**

Résumé

Un indicateur permet de mesurer des grandeurs ou des phénomènes trop compliqués ou trop coûteux à mesurer de manière directe. Lorsqu'il s'agit de biodiversité, les indicateurs sont indispensables au regard de la complexité à avoir une image précise de l'état et de la dynamique des espèces. En forêt, les microhabitats des arbres (*e.g.*cavités, fentes du bois, carpophores de champignons lignicoles) sont considérés comme des indicateurs potentiels de biodiversité, plus spécifiques que des structures telles que le volume de bois mort total. Cependant, les références scientifiques établissant le lien entre métriques de microhabitats et mesures de biodiversité restent rares, et ne concernent la plupart du temps qu'un seul groupe taxonomique. Plus largement, et à l'instar d'autres indicateurs, les microhabitats ne bénéficient pas d'une démarche standardisée permettant de les valider en tant qu'indicateurs de biodiversité forestière.

Ce travail de thèse contribue à cette validation. Il s'articule autour de trois aspects entrant en compte dans la validation d'un indicateur, il s'est agi :

(i) De quantifier et réduire les incertitudes sur les inventaires de microhabitats. A cette fin, une première typologie de référence a été établie, avec pour but de standardiser et d'homogénéiser les relevés de microhabitats. Cette typologie adopte une structure hiérarchique et évolutive, ce qui permet de l'utiliser dans différents contextes. Le biais potentiel lié aux observateurs a également été quantifié, de manière à pouvoir mieux le prendre en compte dans les futurs inventaires ;

(ii) De mieux comprendre les facteurs d'influence des microhabitats aux deux échelles. A l'échelle de l'arbre, l'analyse d'un jeu de données national a permis de généraliser la relation entre caractéristiques individuelles des arbres (espèce, diamètre, vitalité) et le nombre et l'occurrence des microhabitats. A l'échelle de la parcelle forestière, une analyse des densités et des types d'arbres porteurs de microhabitats sur un gradient élargi d'exploitation forestière, comparant zones exploitées et non exploitées, a permis de mettre en évidence le rôle crucial des gros arbres et des arbres morts.

(iii) D'établir le lien entre microhabitats et la diversité de trois groupes taxonomiques au travers d'une approche mobilisant le cadre analytique des modèles d'équations structurelles. Les microhabitats sont médiateurs de l'arrêt de l'exploitation et de structures typiques des vieilles forêts (gros arbres vivants et morts) sur la biodiversité des chauves-souris et des oiseaux, et dans une moindre mesure des coléoptères saproxyliques.

Au final, les microhabitats ne constituent pas un indicateur universel de biodiversité mais ont un rôle complémentaire des autres structures forestières traditionnellement utilisées pour décrire la biodiversité. Ce travail de thèse contribue à préciser leur potentiel indicateur et envisage des pistes de recherche permettant de continuer à valider leur rôle.

Abstract

An indicator is a tool to measure metrics or phenomenons too complex or costly to measure directly. In the case of biodiversity, indicators are essential regarding the complexity to assess species state and dynamics. In forest, tree microhabitats (*e.g.*cavities, cracks in the wood, conks of lignicolous fungi) have been recently considered as a potential biodiversity indicator, with a more specific focus than other structures like deadwood volume. However, scientific references linking tree microhabitat metrics and biodiversity measures are still rare, and limited to a few taxonomic groups. More generally, like other indicators, the validation process of microhabitats as biodiversity indicators is not standardized.

This ph-d thesis contributes to this validation and adresses three aspects included in an indicator validation process. The main aims were to:

(i) Quantify and reduce incertitudes on tree microhabitat inventories. We thus proposed a first reference typology to standardize and homogenize microhabitats inventories. This typology has a hierarchical and evolutive structure, which allows its use in different contexts and for different purposes. We also quantified the potential bias linked to observer effects, in order to better take it into account in future inventories;

(ii) Better understand the influence of different factors on tree microhabitats at two different scales. At the tree scale, through the analysis of a national database, we generalized the relationships between tree characteristics (species, diameter, vitality) and number and occurrence of tree microhabitats. At the stand scale, we analysed the densities and types of microhabitat-bearing trees on an enlarged forest management gradient, comparing strict reserves and managed forests. These two studies evidenced the crucial role of large trees and snags in the provision of tree microhabitats;

(iii) Link tree microhabitats with the biodiversity of three taxonomic groups through the framework of structural equation models. We showed that microhabitats mediate the effects of management abandonment and old-growth forest features (large living and dead trees) on the biodiversity of birds and bats, and to a lesser extent on saproxylic beetles.

In the end, tree microhabitat are not a universal biodiversity indicator but have a complementary role compared to other forest structures traditionally used to assess biodiversity. This ph-d thesis specifies the role of tree microhabitats as biodiversity indicators and proposes further research to continue validating them as such.

Remerciements

Il y a quelques années, j'affirmais avec pas mal d'aplomb que je ne voulais pas faire de thèse. Les collègues présents à cette époque ne se sont pas privés de me rappeler mes incohérences quand, il y a trois ans, j'ai entamé ce travail après de longues années de réflexion. Si ma thèse a été une démarche avant tout personnelle, elle n'a été possible que grâce à l'implication de nombreuses personnes, collègues aussi bien qu'amis, qui ont contribué collectivement et de différentes manières à ce travail. Je tiens à les remercier ici car, sans eux, il est évident que rien n'aurait été possible.

J'ai sans doute un peu parachuté mon sujet sur la tête d'Eric Guilbert, qui a malgré tout accepté de diriger cette thèse, avec enthousiasme et bienveillance. Je le remercie pour ses points réguliers, ses encouragements, ses relectures et son initiation à la grimpe libre dans les arbres. J'espèce que nous continuerons à collaborer de manière aussi constructive à l'avenir et que nous parviendrons enfin à aller mesurer des cavités en haut des arbres !

Frédéric Archaux a accepté d'être mon co-encadrant « de proximité » à Nogent-sur-Vernisson. Toujours présent malgré des obligations professionnelles grandissantes, il a su m'aiguiller et me remotiver à chaque fois que nécessaire. Il m'a également fait une totale confiance pour mener ce travail et a été d'une aide précieuse à chaque fois que j'en ressentais le besoin.

Je remercie Aurélien Besnard et Hervé Jactel pour avoir accepté d'être les rapporteurs de ce travail, ainsi qu'Emilie Andrieu, Jane Lecomte et Romain Julliard pour avoir accepté d'être examinateurs et constituer le jury de thèse.

Une grande majorité des données que j'ai utilisées sont issues du projet « Gestion Forestière, Naturalité et Biodiversité », coordonné par Irstea, l'Office National des Forêts et les Réserves Naturelles de France. Ce projet collaboratif a impliqué fortement les gestionnaires locaux et les réseaux naturalistes de l'Office, sans qui je n'aurais pu bénéficier de telles données. Ils sont nombreux, je ne les connais pas tous et j'en oublie sans doute, mais qu'ils soient remerciés pour leur implication et leur travail et pour les discussions improvisées sur le terrain, au détour d'un chemin forestier : Thomas Barnouin, Daniel Barré, I. Bassi, Jérome Bernard, B. Blaise, Jean-Jacques Boutteaux, Sebastien Coulette, T. Darnis, Pascal Denis, B. Devaux, Laurent Domergue, Caroline Druesne, Sylvain Ducroux, Stéphane Dumas, Bruno Fauvel, Thierry Freund, Benoit Fritsch, Vincent Godreau, J.-P. Gollé, Eric Jensel, Lydie Lallement, Romaric Lecomte, Johann Leseure, Jacques L'Huillier, Frédéric Malgouyres, C. Marck, Philippe Millarakis, Carl Moliard, Thierry Noblecourt, Benoit Nusillard, S. Pauvert, Alain Perthuis, Daniel Reboul, Johann Rosset, Elisabeth Royer, Laurent Servières, G. Sivry, Fabien Soldati, Jean-Luc Témoin, Jérémie Terracol, Laurent Tillon, Hervé Tournier et R. Truckenwald.

Merci à Nicolas Debaive et Olivier Gilg de m'avoir fait confiance pour l'analyse des données des réserves naturelles et biologiques.

Il y a eu également le test d'effet observateur auquel se sont pliés de valeureux volontaires pour les journées en forêt de Fontainebleau. Je les remercie pour leur sérieux et leur bonne humeur lors de ce travail parfois un peu fastidieux : Pénélope Anselle, Dominique Ballon, Isabelle Bilger, Adélie Chevalier, Gilles Defour, Laurent Larrieu, Aurore Lassauce, Benoit Nusillard, Mélanie Picard, Anthony Pouzerat et Anne Villemey.

Parmi les collaborations particulièrement fructueuses, le travail entrepris pas les collègues allemands de l'Institut Forestier Européen, et leur prise en main de la diffusion et de la popularisation des microhabitats au niveau européen est remarquable. Je remercie Daniel Kraus et Frank Krumm pour leur confiance et les bons moments passés sur le terrain. Dans ce groupe, il y a aussi les collègues qui ont contribué – non sans mal – à la publication de la typologie présentée dans cette thèse. Ce travail a été particulièrement stimulant, notamment lors du Workshop organisé à Nogent et je tiens à tous les

remercier pour les discussions fertiles et le travail collaboratif : Rita Bütler, Thibault Lachat, Laurent Larrieu, Alexa K. Michel, Baptiste Regnery, Kris Vandekerkhove et Susanne Winter.

Bien entendu, un tel travail ne peut s'envisager sereinement que dans un cadre propice et scientifiquement motivant. C'est le cas de l'unité « Ecosystèmes Forestiers » à Nogent sur Vernisson et je tenais à remercier tous les membres de cette communauté pour ce qu'ils ont pu m'apporter durant ces années.

Au-delà de cet environnement favorable, il y a bien sûr ces liens particuliers que l'on finit par tisser avec certaines personnes et qui agrémentent le quotidien pour le rendre agréable. Je remercie Gwendoline, Marie et Fabien, pour les nombreuses discussions sur les microhabitats et les cavités, notamment lors du célèbre « Club Cavité » fondé en 2018. Hilaire a toujours été là pour régler mes problèmes de systèmes de projection SIG, faire de la bota ou une pause café, jouer de la musique ou simplement discuter autour de sujets variés et ésotériques. Il a également accepté de relire mon manuscrit avec enthousiasme et efficacité et je l'en remercie chaleureusement. Sylvie est la personne indispensable au bon fonctionnement administratif d'un service, elle est aussi très à l'écoute et je la remercie pour tous les échanges qu'on a pu avoir.

Dans cette histoire de microhabitats, il y a aussi les stagiaires – « mes » stagiaires – qui ont contribué de manière plus que significative au développement de cette problématique et à ce travail de thèse. Aurélie a été celle qui a lancé le sujet en 2009 au travers d'un stage de grande qualité et parfois acrobatique (pour elle). Aujourd'hui encore, je me réfère souvent à son travail tant elle était en avance sur ce que je savais faire à cette époque. Cette thèse aurait largement pu être la sienne. Pauline a organisé avec flegme le test d'effet opérateur et contribué aux premières analyses du lien entre microhabitats et biodiversité. Son travail reste également une pière angulaire de cette thèse. Solène, que j'ai réussi à attirer dans les filets des microhabitats nogentais, a plus que défriché les analyses taxonomiques et m'a ainsi permis d'avancer au-delà de ce que j'espèrais sur cette partie. Un remerciement spécial pour Caroline et ses heures de SIG à démêler les arcanes du projet et ses données tentaculaires.

Laura et Camille ont eu le « privilège » d'être les stagiaires d'un thésard sarcastique en dernière année, lors de ses derniers mois de rédaction. Du coup, elles ont dû subir la relecture d'un manuscrit apparemment pas toujours très clair. Merci à Laura pour ses relectures attentives et sans concessions, elle a contribué à l'amélioration des enchainements logiques de ce travail. Merci à Camille qui, grâce à un esprit critique sans limites et par plusieurs relectures pertinentes et détaillées, m'a permis de fluidifier ce manuscrit et a levé des blocages alors insurmontables. J'espère qu'on se retrouvera souvent au pied d'un arbre à cavité de pic noir et que nos projets seront fructueux.

Anne est l'amie qui, depuis que l'on s'est rencontrés à Nogent, a su être présente à chaque moment important de ma vie, à la fois pour discuter d'écologie, de cuisine, de randonnée ou de papillons. Elle aussi a subi une relecture du manuscrit et m'a apporté ses conseils lumineux. Elle était aussi là pour m'écouter dans des moments difficiles avec beaucoup de finesse, de tact et de compréhension.

Les « amis de Nogent » sont nombreux et sans eux, la vie dans ce petit village serait monotone. Merci à Agnès R., Cécile, Ushma, Ugoline, Jordan, Philippe, Richard, Thomas, et les « anciens » Marie, Hélène, Océane, Fab, Fred, et tous ceux que j'oublie pour les séances de sport (parfois difficiles), les soirées, les pauses et les litres de café.

Merci enfin à Agnès, qui m'a toujours encouragé et accompagné dans mes projets personnels et professionnels, avec une patience et une gentillesse incroyables. Elle a toujours su trouver les mots pour me rassurer et, même dans ces moments qui jalonnent d'embuches une vie à deux, a toujours su comprendre et écouter avec beaucoup d'affection et de bienveillance.


indicateur
biodiversité
microhabitats
processus
validation
espèces
entre
lien
gestion
plus
forestière
diversité
travail
scientifique
arbres
bois
forêt
données
exemple
politiques
exploitation
influence
comme
Europe
scientifiques
critères
indicandum
cadre
thèse
plusieurs
facteurs
cette
être
autres
deux
types
habitats
aussi
fait
cas

microhabitat
tree
forest
biodiversity
species
cavities
large
types
living
strict
dead
reserves
observer
effect
management
higher
number
densities
also
may
cavity
trunk
deadwood
groups
total
structural
used
woodpecker
standing
significantly
studies
characteristics
managed
fungi
observers
diameter
different
data

Valorisations

Articles scientifiques à comité de lecture

Larrieu, L., **Paillet, Y.**, Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A., Regnery, B., Vandekerkhove, K. (2018). Tree related microhabitats in the temperate and Mediterranean European forests: a hierarchical typology for inventories standardization. *Ecological Indicators* 84: 194-207.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F., Gosselin, F. (2015) Strong observer effect on tree microhabitats censuses: a case study in a French lowland forest. *Ecological Indicators* 49: 14-23.

Paillet, Y., Debaive, N., Archaux, F., Boulanger, V., Gilg, O., Guilbert, E. (in prep). Nothing else matters? A nationwide study of microhabitat drivers at the tree scale. *bioRxiv* 335836, doi: https://doi.org/10.1101/335836.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F. Guilbert, E. (2017). Snags and large trees drive higher tree microhabitat densities in strict forest reserves. *Forest Ecology and Management* 389: 176-186.

Paillet, Y., Archaux, F., Du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F. Guilbert, E. (sous presse). The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.13181

Kozák, D., Mikoláš, M., Svitok, M., Bače, R., **Paillet, Y.**, Larrieu, L., Nagel, T. A., Begovič, K., Čada, V., Diku, A., Frankovič, M., Janda, P., Kameniar, O., Keren, S. Kjučukov, P., Lábusová, J., Langbehn, T., Mikac, S., Morrissey, R. C., Nováková, M., Schurrman, J. S., Svobodová, K., Synek, M., Teodosiu, M., Toromani, E., Trotsiuk, V., Vítková, L., Svoboda, M. (2018). Profile of tree-related microhabitats in European primary beech-dominated forests. *Forest Ecology and Management* 429: 363-374 [Hors manuscrit, *cf.* Annexes E]

Communications orales

Paillet, Y., Du Puy, S., Archaux, F., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E. (2017) The indicator side of tree microhabitats: a multi-taxonomic approach. In: *1st International Conference on Community Ecology (ComEc)*, Budapest, Hungary, September 28-29, 2017.

Paillet, Y., Bouvet, A., Archaux, F., Tillon, L, Denis, P., Gilg, O., Gosselin, F., Guilbert, E. (2017). Deadwood is the main driver of bird and bat communities in strict forest reserves. In: *4th Young National History Scientists' Meeting*. Paris, France, February 7-11, 2017.

Préambule

Le Grand indicateur (*Indicator indicator*) est un oiseau qui vit dans différentes régions d'Afrique subsaharienne. Apparenté aux pics (il appartient à l'ordre des piciformes), il mesure une vingtaine de centimètres de long et est un des rares oiseaux capables de digérer la cire d'abeille. Il est connu pour guider les chasseurs de miel vers les nids d'abeilles en forêt. Lorsque le Grand indicateur découvre un nid d'abeilles, il vole vers un chemin à la recherche d'humains et tente d'attirer leur attention en battant des ailes et en poussant des cris puissants. Lorsqu'un humain le suit, il vole devant lui jusqu'au nid d'abeille où il se met à chanter. Ces nids se trouvent le plus souvent dans des cavités d'arbres creux, mais aussi entre des rochers, enfouis dans le sol ou sur d'anciennes termitières. Dans les arbres, les chasseurs recueillent le miel en enfumant le nid. Une fois le miel récupéré, le Grand indicateur peut alors se nourrir des restes de cire laissés par les chasseurs. Cet oiseau est appelé « *Gbassara* », « *Sazou* », « *Morok* », « *Sengo* » ou « *Fonton* » dans les différentes régions d'Afrique où on lui connait ce comportement. Des études récentes rapportent que les chasseurs de miel trouvent des nids d'abeilles de trois à six fois plus rapidement lorsqu'ils bénéficient de l'aide de l'oiseau. C'est un des rares cas documentés de mutualisme, c'est-à-dire une association qui bénéficie aux deux partenaires, entre un non-humain et un humain.

Cette histoire a été racontée par Jean-Claude Ameisen sur France Inter, dans l'émission « Sur les Epaules de Darwin » diffusée la première fois le 3 septembre 2016. J'ai choisi de la retranscrire car elle évoque, sous forme métaphorique et en lien avec mon travail de thèse, la façon dont les indicateurs (environnementaux) sont validés. Le Grand indicateur est « l'outil » qui permet aux chasseurs de miel d'améliorer leur récolte, car il détecte d'une façon plus efficace qu'eux les nids d'abeille. Le Grand indicateur est un outil robuste, puisqu'il est utilisé par plusieurs tribus à travers l'Afrique. Il a été validé par l'usage qu'en font les chasseurs et par les bénéfices qu'ils en retirent dans leur activité. L'oiseau lui-même profite de cette alliance – ce qui n'est pas souvent le cas pour des indicateurs plus « théoriques ». Il est aussi question de forêt et d'arbres creux où vivent des abeilles, deux autres éléments qui ont toute leur place dans mon travail de thèse.

Cette histoire illustre « *les liens invisibles qui tissent la trame* [des] *relations entre les êtres vivants* »*, elle montre également que les processus de construction et de validation d'indicateurs (environnementaux) relient et impliquent des acteurs issus de mondes différents : usagers et chercheurs, humains et non-humains. « *Cela fait partie de l'université de la forêt, il faut y vivre pour cultiver ses sens* »* : c'est un petit bout de cette université que je vous invite à visiter dans cette thèse.

** Citations tirées de l'émission de J-C. Ameisen.*

Table des matières

Liste des Figures

Liste des Tableaux

Chapitre 1 - Introduction : les microhabitats, indicateurs de biodiversité ?

1.1. Qu'est-ce qu'un indicateur et comment le valide-t-on ?

1.1.1 Indicateur, indicandum, indices

Dans sa définition classique, un indicateur permet de mesurer des grandeurs ou des phénomènes trop compliqués (ou coûteux) à mesurer de manière directe (*e.g.*Heink & Kowarik, 2010a). Un indicateur est réputé apporter des informations sur des problématiques de large ampleur, ou rendre perceptibles des tendances ou des phénomènes qui ne sont pas immédiatement détectables. En ce sens, l'intérêt d'un indicateur donné s'étend au-delà de ce qui est effectivement mesuré pour englober un phénomène plus large (Hammond et al., 1995; Niemeijer & de Groot, 2008). Un indicateur n'a de sens que par rapport à l'objet ou au phénomène qu'il indique, que l'on nomme l'*indicandum* (Heink & Kowarik, 2010a). Les indicateurs se différencient des indices – ou métriques – par le fait que ces derniers n'ont pas d'*indicandum*, mais sont absolus. Ainsi, c'est la combinaison entre un indice et un *indicandum* qui constitue l'indicateur : l'indicateur ne devient tel que lorsque l'*indicandum* est clairement défini et que le lien avec l'indice mesuré est précisé. Ces définitions seront utilisées tout au long de ce travail. La distinction terminologique entre indicateur et indice est importante car l'utilisation du terme « indice » (ou index, Moriarty et al., 2018) peut se référer à d'autres mesures, notamment à des métriques composites, calculées à partir de plusieurs indices, comme l'indice « Planète vivante » utilisé par le Fonds Mondial pour la Nature (Tittensor et al., 2014).

Dans le cas des indicateurs écologiques ou environnementaux, auxquels je m'intéresse dans cette thèse, les *indicanda* sont des phénomènes ou des grandeurs physiques ou biologiques (Levrel et al., 2007) et les indices utilisés sont divers. Par exemple, le nombre d'espèces ou d'individus au sein d'une communauté sont des indices classiques en écologie (richesse et abondance) qui peuvent servir d'indicateurs de conditions environnementales, comme un niveau de pollution aquatique (*e.g.*Bouleau, 2016).

Le lien indicateur - *indicandum* prend une place fondamentale dans le processus de validation scientifique des indicateurs, notamment lorsqu'il s'agit d'indicateurs décrivant des variations de biodiversité (Heink & Kowarik, 2010a). Cela a des implications à la fois théoriques et statistiques. Ce lien n'est pas toujours forcément explicité dans les processus de rapportages internationaux (*e.g.*Feest, 2013). Il semble donc intéressant de comprendre comment et pourquoi les indicateurs sont choisis et validés.

1.1.2 Des indicateurs pour quoi faire ? Validation des indicateurs environnementaux à la croisée de l'écologie et des sciences sociales

1.1.2.1 Des objets frontières

L'objet indicateur est à l'interface de plusieurs disciplines et utilisé par des sphères d'acteurs différentes (Angelstam et al., 2013; Heink & Kowarik, 2010a; Rametsteiner et al., 2011; Turnhout et al., 2007). Souvent construits par des scientifiques, issus de la biologie au sens large (Turnhout et al., 2007), les indicateurs environnementaux ont presque toujours une finalité appliquée à la gestion des écosystèmes ou à l'évaluation – et éventuellement au pilotage – des politiques publiques. Par exemple, les inventaires forestiers nationaux produisent des indicateurs de ressource et de récoltes forestières utiles à la fois aux gestionnaires et aux politiques désirant développer une filière bois (Forest Europe, 2015a). Cette position intermédiaire entre science et acteurs publiques (non-scientifiques) renvoie les indicateurs à la notion sociologique d'objet frontière définie initialement par Star and Griesemer (1989). Ils assurent la médiation et le dialogue entre acteurs de différentes origines avec des intérêts différents (Trompette & Vinck, 2009; Turnhout, 2009). De ce fait, ils doivent disposer d'un ensemble de propriétés qui leur permettent de s'adapter et d'assurer la communication entre des mondes aux

référentiels différents. Cela comprend notamment l'existence d'une structure minimale de connaissance incluant un ensemble de conventions, de standards et de normes (en particulier sur les méthodes utilisées pour produire l'objet, Trompette & Vinck, 2009). Du fait de cette position intermédiaire, les indicateurs sont aussi l'objet de controverses et de négociations qui dépassent le cadre purement scientifique de leur conception (Angelstam et al., 2013; Rametsteiner et al., 2011).

Cela amène à s'interroger sur les processus de validation et les critères qui concourent au choix et à l'utilisation d'un indicateur dans un contexte donné. Ces critères relèvent à la fois des sciences écologiques et des sciences politiques. Ainsi, leur processus de validation ne relève pas uniquement de la capacité d'un indicateur à décrire les variations de son *indicandum* – et donc pas uniquement d'une forme de validation statistique issue d'une analyse mobilisant des données biologiques ou écologiques. Ce processus questionne avant tout la façon dont ils sont validés par un groupe d'acteurs dans un cadre donné.

Le terme de « validation » est en lui-même polysémique et ambigu, car il dépend à la fois, dans le cas des indicateurs, de la discipline scientifique mobilisée et du point de vue théorique adopté (notamment écologie vs sciences sociales), mais aussi de l'ensemble d'acteurs concernés par ce processus (*e.g.* scientifiques vs décideurs). On peut néanmoins retenir la définition proposée par Rykiel (1996) dans le cas des modèles en écologie et reprise récemment par Moriarty et al. (2018) : la validation est un processus qui établit qu'un indicateur remplit des critères de performance choisis dans un contexte spécifique. Ce processus nécessite au préalable de définir les objectifs et les questions auxquelles un indicateur doit répondre, les critères de performance et le contexte dans lequel ils s'appliquent. Ces objectifs et les questions qui en découlent sont en général affinés par une inscription dans un cadre d'analyse qui permet à la fois de catégoriser un ensemble d'indicateurs et d'analyser les liens (causaux) qui les relient (Feest, 2013; Niemeijer & de Groot, 2008).

1.1.2.2 Définir des objectifs

La position des indicateurs à l'interface entre différents mondes pose la question de leur utilisation. Dans leur synthèse, Heink and Kowarik (2010a) identifient différents usages pour les indicateurs en écologie et en planification environnementale. Les indicateurs peuvent soit être descriptifs de l'état d'un système et de son évolution ou avoir une portée normative, quand ils sont utilisés pour évaluer des changements et fixer des objectifs en référence à un système de valeurs (voir aussi par exemple Angelstam et al., 2013). Ce dernier type est principalement utilisé dans une optique de gestion ou de mise en œuvre et d'évaluation de politiques publiques, en particulier par la définition de seuils (Herrmann et al., 2003; Samhouri et al., 2010). Un même indicateur peut être indifféremment utilisé de manière descriptive ou normative en fonction de l'objectif recherché : par exemple, le volume de bois mort par hectare est utilisé pour décrire la biodiversité (dite saproxylique) qui en dépend; lorsque des seuils de volume sont fixés, dans une optique de conservation d'espèces (*e.g.*Müller & Bütler, 2010), l'indicateur bois mort acquiert une portée normative. Les auteurs mentionnent également l'existence d'indicateurs hybrides avec une distinction pas toujours explicite du caractère descriptif ou normatif (Heink & Kowarik, 2010a; Heink & Kowarik, 2010b). Parmi les indicateurs normatifs, on peut faire une distinction supplémentaire entre des indicateurs prescriptifs qui stipulent un état à atteindre et des indicateurs évaluatifs qui permettent d'établir si l'objectif désiré a été atteint (c'est typiquement le cas des indicateurs d'état de conservation des habitats, Maciejewski et al., 2016).

1.1.2.3 Nécessité d'un cadre d'analyse

L'évaluation environnementale repose rarement sur un indicateur unique, mais plutôt sur un ensemble d'indicateurs inscrits dans une cadre analytique. Le plus utilisé pour l'évaluation environnementale est le système Force Motrice – Pression – Etat – Impact – Réponse (Figure 1), ou son équivalent simplifié Pression – Etat – Réponse (EEA, 1999). Initialement développé par

l'organisation pour la Coopération Economique et le Développement (OECD, 1994), ce cadre a été utilisé par les nations unies (UNEP, 1997, 2007) et l'Agence Européenne de l'environnement (EEA, 1999) pour établir le lien entre activités humaines et environnement. Il permet de regrouper les indicateurs en fonction de l'information qu'ils fournissent sur une cible donnée (par exemple, la biodiversité ou la gestion forestière durable) et les inscrit dans un système causal (Figure 1). Il est ainsi possible, par exemple, d'identifier les pressions exercées sur une cible donnée et d'apporter des réponses (politiques, sociétales, de gestion) pour améliorer son état.

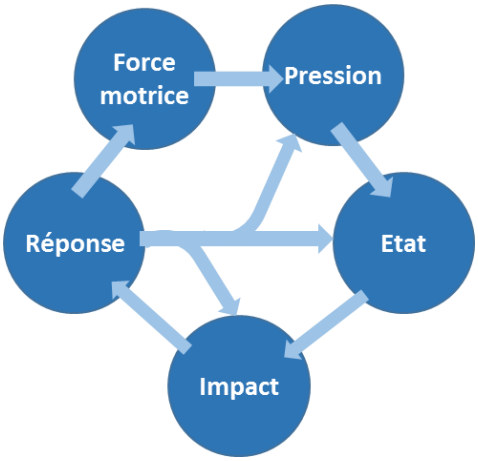


Figure 1 : Schématisation du cadre d'analyse Force motrice – Pression – Etat – Impact – Réponse. Il assume la chaîne causale suivante où les relations sont illustrées par les flèches : les forces motrices (secteur économique, activités humaines) exercent des pressions (émissions, déchets) qui conditionnent l'état de l'écosystème (physique, chimique et biologique), ont un impact sur le bien être humain et amènent à des réponses politiques (priorisation, établissement d'objectifs).

Ce cadre n'est pas utilisé pour sélectionner – et encore moins valider – des indicateurs (Niemeijer & de Groot, 2008), mais rationalise un ensemble d'indicateurs traitant d'un même sujet dans un modèle relationnel. Le processus de validation à proprement parler vient ensuite.

1.1.2.4 Quels critères de validation ?

Une fois les objectifs définis, les questions identifiées et le cadre analytique posé, le processus de validation prend différentes formes. Il n'existe en effet pas de processus standardisé de validation des indicateurs environnementaux (*e.g.* Bockstaller & Girardin, 2003). Cette absence de processus explicite de validation fait d'ailleurs l'objet de nombreuses critiques (*e.g.* Dale & Beyeler, 2001; Heink & Kowarik, 2010b; Moriarty et al., 2018). Cependant, Niemeijer and de Groot (2008), analysant plusieurs systèmes d'indicateurs et de rapportage, résument les critères utilisés pour la sélection et l'utilisation d'indicateurs environnementaux. Je les résume ici car ils permettent de définir un cadre de validation. Ils relèvent de plusieurs dimensions :

(i) Scientifique : les indicateurs doivent s'appuyer sur des bases théoriques et empiriques solides. De fait, la validation d'un indicateur donné requiert l'existence d'un lien théorique, causal ou fonctionnel avec son *indicandum*. En pratique, la pertinence du lien entre indicateur et *indicandum* est testée au travers de méthodes statistiques qui permettent d'évaluer une corrélation entre des variables réponses (l'*indicandum*) et explicatives (l'indicateur potentiel, *cf.* la synthèse de Heink & Kowarik, 2010b). Un indicateur est en général jugé pertinent si la corrélation avec son indicateur est significative (au seuil choisi) et forte (*e.g.* Niemela, 2000). Cette approche par corrélation a des conséquences implicites sur la validation des indicateurs. En effet, si le niveau de significativité est la plupart du temps choisi par convention (*i.e.* seuil de 5%), le niveau à partir duquel une corrélation est jugée « forte » est rarement précisé. Dans leur synthèse

sur les indicateurs forestiers de biodiversité, Gao et al. (2015) utilisent une approche par décompte pour évaluer comment le potentiel indicateur est supporté par la preuve scientifique : le potentiel indicateur est jugé respectivement faible, moyen ou fort si la littérature fait état d'une, deux ou plus de trois corrélations sans résultat contradictoire. Ces auteurs n'utilisent que le nombre de corrélations significatives sans juger de la force de la relation (voir Barbier et al., 2009 pour un contre-exemple) ;

(ii) Historique : les indicateurs doivent si possible mobiliser des données existantes, solides et validées. Cette forme de construction (le « recyclage », *e.g.* Bouleau et al., 2016) est très largement utilisée, notamment dans les processus de rapportage pour des raisons pratiques et de coût évidentes. Cette pratique montre néanmoins des limites en termes de représentativité : dans le cas de la biodiversité forestière, les indicateurs traitant des taxons sur lesquels portent les enjeux de gestion (principalement les espèces saproxyliques) sont très peu représentés (Gosselin et al., 2012; Paillet, 2017) ;

(iii) Systémique et intrinsèque : ces dimensions relèvent de la construction même d'un indicateur et des propriétés qui en découlent. On peut retenir en particulier que la robustesse (ou sa portabilité), c'est-à-dire la validité d'un indicateur dans des contextes différents, est un critère important : par exemple, le lien entre volume de bois mort et diversité des organismes associés persiste-t-il quand les conditions écologiques changent (*cf.* Lassauce et al., 2011) ? ;

(iv) Pratique et financière : la prise de mesure permettant de renseigner un indicateur doit être réaliste et si possible demander des niveaux de compétences raisonnables. De même que la construction d'indicateurs sur données existantes, cette dimension contraint fortement l'innovation et le recueil de données nouvelles, notamment lorsqu'elles demandent des compétences fortes, comme c'est le cas de certains relevés taxonomiques. Il est intéressant de noter que l'analyse de Niemeijer and de Groot (2008) porte principalement sur des processus politiques. Cela transparaît au travers d'une approche pragmatique et à coût limité ;

(v) Politique et gestion : cette dimension fait le lien avec les utilisateurs finaux des indicateurs et leur accessibilité pour un public qui ne serait pas (ou moins) scientifique que les concepteurs.

Ainsi, si les principes généraux de validation peuvent être objectivés, l'évaluation pratique des performances des critères de validation soulève des questions méthodologiques, *a fortiori* parce que tous les critères ne sont pas forcément quantifiables. Par contre, la validation des indicateurs construits pour permettre une description scientifique de la biodiversité repose presque exclusivement sur le point (i) développé ci-dessus (Heink & Kowarik, 2010b) et constitue le cœur de mon travail de thèse.

1.2. La nécessité d'indicateurs de biodiversité scientifiquement construits

Le terme de biodiversité comprend la diversité du vivant au niveaux des gènes, des espèces et des écosystèmes (Secretariat of the Convention on Biological Diversity, 2006). Popularisée depuis la conférence mondiale sur la diversité biologique (à Rio en 1992), la mesure de la biodiversité est rendue difficile par la multitude des dimensions qui la composent, ainsi que le coût des techniques et de la main d'œuvre nécessaires pour l'appréhender de manière exhaustive. Face à son érosion croissante (Butchart et al., 2010; Delbaere, 2004; Tittensor et al., 2014), une problématique liée à la biodiversité a émergé sur la scène internationale et nécessite d'acquérir une connaissance robuste de l'état et de la dynamique de la biodiversité. De nombreuses initiatives de suivi ont vu le jour au cours des trente dernières années, notamment sous les auspices du groupe d'observation de la Terre GEO, en particulier l'initiative GEOBON (Scholes et al., 2008; Scholes et al., 2012). Ces travaux ont aussi donné naissance à des processus de rapportage : (i) tous milieux, comme celui mené par l'Agence Européenne de l'Environnement (EEA, 1999) ; ou (ii) sectoriels comme la directive cadre européenne sur l'eau (*e.g.*

Bouleau, 2016) ou le suivi de la gestion forestière durable (Forest Europe, 2015a). Malgré la valeur incontestable de ces efforts de structuration et des données à large échelle qui ont été produites, les facteurs explicatifs des dynamiques observées ont souvent été identifiés à des échelles très larges, basés sur des données paysagères ou des modèles climatiques (Jiguet et al., 2012), alors que des données plus précises de gestion sont rarement prises en compte et ne permettent pas d'action ciblée concrète (*e.g.* Paillet, 2017).

La connaissance de l'état et de la dynamique de la biodiversité a donc nécessité la mise en œuvre d'indicateurs dédiés. La validation scientifique de ce lien repose avant tout sur des fondements théoriques solides, même si cet aspect ne constitue qu'un des critères de validation (Niemeijer & de Groot, 2008). Ainsi, la conception et la mise en œuvre d'indicateurs de biodiversité peut être basée sur le lien entre espèces (co-occurrence) ou entre espèces et habitat(s) favorable(s). Il convient donc ici de rappeler les fondamentaux des théories d'assemblage des communautés de manière à comprendre quelles sont leurs implications pour la définition d'indicateurs.

1.2.1 Bases théoriques des relations entre espèces, communautés et habitats

1.2.1.1 Relation aire-espèces

La relation entre les espèces et leur habitat – aussi connue sous le nom de relation aire-espèces – est au départ une constatation empirique. Elle émane de l'observation de la relation positive entre nombre d'espèces et surface de la région observée, notamment sur les îles isolées dans différentes parties du globe : la multiplication par 10 de la surface de l'île double la richesse en espèces (*e.g.* Chisholm et al., 2018). Cette relation est ensuite formalisée mathématiquement par une fonction puissance dont plusieurs formulations ont été proposées, mais qui a globalement la forme illustrée par la Figure 2a. Sur une échelle log-log, cette équation se linéarise ce qui permet une modélisation facile de la relation (Figure 2b), *cf. e.g.* Fahrig (2013).

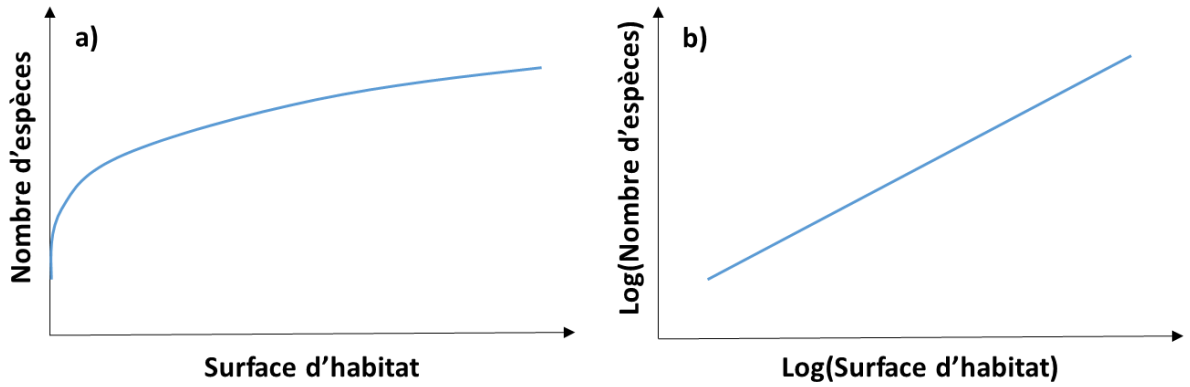


Figure 2 : Illustration de la relation aire-espèce sur une échelle arithmétique (a) et sur une échelle log-log (b)

Les trois principaux mécanismes évoqués pour justifier cette relation sont (Connor & McCoy, 2001) :

- L'hypothèse de diversité d'habitats : les habitats de grandes surfaces ont plus de chances d'être plus diversifiés que des habitats de plus petites surfaces, et hébergent donc plus d'espèces ;
- L'hypothèse de surface en tant que telle : la probabilité d'extinction est plus faible dans les habitats de grandes surfaces que dans les petits ;
- L'hypothèse d'échantillonnage passif : les habitats de grandes surfaces reçoivent plus d'espèces colonisatrices que les petits.

Initialement formulée pour des îles isolées dans l'océan, la relation aire-espèce a ensuite été appliquée avec constance à de nombreux cas de relations entre espèces et habitat, et en intégrant les variations

d'un niveau de ressource pertinent pour une espèce donnée, en lieu et place de la surface des îles (Bouget, 2013).

1.2.1.2 Théorie de la niche

La niche écologique est définie initialement par Grinnell (1917) comme la réponse d'une espèce à un ensemble de conditions environnementales, puis par Elton (1927) comme l'impact d'une espèce sur son environnement. Ces deux définitions sont unifiées et étendues par Hutchinson (1957) qui distingue la niche fondamentale – constituée uniquement des caractéristiques abiotiques – et la niche réalisée – qui intègre interactions biotiques et processus de colonisation / extinction des espèces. La coexistence des espèces au sein d'une communauté dépend donc de leur capacité à exploiter les ressources de la niche à laquelle elles appartiennent, ce qui conditionne également la compétition entre espèces dont les niches se chevauchent. Ainsi, la niche recouvre un ensemble de conditions biotiques et abiotiques. Il en découle deux hypothèses qui conditionnent, au sein d'une niche donnée, la coexistence d'espèces dans la communauté et qui étendent la relation aire-espèce :

- L'hypothèse d'hétérogénéité (Tews et al., 2004) postule qu'une augmentation de diversité des habitats entraîne une augmentation de la diversité en espèces dans la lignée de l'hypothèse de diversité d'habitats. La notion d'hétérogénéité intègre à la fois des composantes spatiales et temporelles, et donc des notions aussi bien statiques (*e.g.* l'agencement spatial d'un peuplement forestier) que dynamiques (*e.g.* l'évolution au cours du temps de cet agencement) ;
- L'hypothèse énergie – espèce (Wright, 1983) postule que plus la quantité d'énergie – et donc de ressource exploitable – est disponible dans un système, plus le système peut accueillir d'espèces.

En pratique, hors conditions expérimentales laborieuses *in natura*, il est difficile de séparer les effets liés à ces deux hypothèses, une augmentation de ressource induisant très souvent une hétérogénéité spatiale, mais aussi de la qualité et de la diversité des ressources disponibles. Il semble cependant que la diversité ait un rôle prépondérant sur la quantité (voir *e.g.* Seibold et al., 2016 dans le cas de la relation bois mort – coléoptères saproxyliques).

1.2.1.3 Biogéographie insulaire

Le corpus théorique – partiel – résumé ci-dessus a finalement été étendu par MacArthur and Wilson (1967) qui y intègrent une dimension spatiale, en se basant toujours sur l'étude d'îles plus ou moins isolées du continent. La théorie de la biogéographie insulaire – ou d'équilibre dynamique – postule que plus une île est éloignée du continent (qui constitue une source d'espèces), plus elle sera pauvre en espèces, toutes choses étant égales par ailleurs (notamment la taille de l'île). Cette théorie a évolué et a été complétée pour intégrer des processus dynamiques de succession – extinction – colonisation (métapopulations, Hanski, 1998; Levins, 1969), des notions de populations sources et puits (Pulliam, 1988), et l'influence d'une matrice non homogène sur les processus de dispersion au travers de l'approche paysage (Forman & Godron, 1986; Turner, 1989). Finalement, Lortie et al. (2004) proposent d'unifier ces notions issues de différentes disciplines (biogéographie, écologie des communautés, écologie du paysage) pour expliquer les assemblages des communautés. Le modèle des filtres emboîtés postule qu'à partir d'un pool régional d'espèces, différents filtres environnementaux s'appliquent pour aboutir à une communauté d'espèces : d'abord un filtre biogéographique (distance entre sites et corridors), puis un filtre abiotique (conditions climatiques, perturbations, hétérogénéité) et enfin un filtre biotique (interactions).

1.2.2 Implications pour la définition des indicateurs de biodiversité

La formalisation conceptuelle et mathématique des règles d'assemblage des communautés a influencé et orienté la recherche en écologie au cours des cinquante dernières années. Cette influence se répercute également sur les indicateurs de biodiversité.

Sur la base de la co-occurrence d'espèces, certains indicateurs peuvent être qualifiés de « directs » ou « taxonomiques ». Ils correspondent à des espèces ou des groupes d'espèces qui représentent la diversité d'un groupe d'espèce plus large (*e.g.* guildes), ou de propriétés de l'écosystème (on parle aussi de « bioindicateurs »). Il s'agit notamment d'espèces dites « indicatrices » pour lesquelles de nombreux travaux ont été publiés (*e.g.* De Cáceres & Legendre, 2009; Ranius, 2002; Roberge & Angelstam, 2006) ou d'indices basés sur des listes d'espèces (*e.g.* le « Red List Index » ou le « Living Planet Index », Vačkář et al., 2012). Cette notion a été étendue en biologie de la conservation par le concept d'espèce parapluie, dont la conservation influence positivement d'autres espèces (Roberge & Angelstam, 2004). Ces espèces ont en général des exigences fortes en termes de domaine vital et de qualité d'habitat, comme par exemple des prédateurs en haut de la chaine alimentaire (Loup, Ours).

Sur la base de la relation entre habitat (ressource) et espèces, d'autres indicateurs peuvent être qualifiés d'« indirects ». Ils postulent que les propriétés de l'habitat permettent de décrire l'état et la dynamique des espèces (individuelles, guildes ou communautés). Ces indicateurs présentent l'avantage non négligeable d'être plus faciles (et souvent moins coûteux) à mesurer que leur *indicandum*, ce qui est intéressant dans le cas de la biodiversité. Ils reposent sur des composantes de l'écosystème qui sont utilisées comme « proxies » d'une espèce ou d'un groupe d'espèces d'un ou plusieurs taxons donnés. Ces composantes sont classées en trois catégories (Angelstam et al., 2013; Dale & Beyeler, 2001; Noss, 1990) :

(i) la composition fait référence à l'identité et la diversité des éléments (à la fois génétique, spécifique et écosystémique, *e.g.* diversité paysagère d'habitats à l'échelle d'une région) ;
(ii) la structure fait référence à l'agencement spatial de ces différents éléments de l'écosystème (*e.g.* la distribution des diamètres des arbres en forêt) ;
(iii) le fonctionnement fait référence à un processus biologique à l'œuvre dans un écosystème donné (*e.g.* production primaire, décomposition).

Ainsi, un indicateur de biodiversité utilisé par l'Agence Européenne de l'Environnement concerne le volume de bois mort, élément de structure forestière relevé par les inventaires forestiers et qui constitue un proxy structural de la biodiversité des espèces dites saproxyliques (*i.e.* qui dépendent du bois mort). Les systèmes de suivi tel celui de cette Agence combinent en général un ensemble d'indicateurs informant sur un *indicandum* (ou une problématique plus large) commun.

1.3. Quels suivis et indicateurs de biodiversité pour la forêt ?

La mise en place de processus d'évaluation de la biodiversité basés sur un système d'indicateurs répond à un objectif général d'endiguer son érosion d'ici 2020 (Feest, 2013), au travers par exemple d'une gestion durable de l'écosystème forestier (Inhaizer et al., 2013). En forêt, les suivis bénéficient de l'apport des inventaires forestiers nationaux, sur lesquels de nombreux dispositifs de recueil de données de biodiversité sont fondés (Lee et al., 2005; Tomppo et al., 2010). Ainsi, les indicateurs forestiers qui ont été développés récemment reposent essentiellement sur des indicateurs indirects utilisant la composition et la structure forestières (*e.g.* Forest Europe, 2015a; Lindenmayer et al., 2000). Il existe plusieurs processus de suivi et de rapportage concernant la biodiversité (forestière) qui utilisent des indicateurs. Je prends ici deux exemples de démarches au niveau international.

1.3.1 Deux exemples européens

Le premier exemple concerne le processus de rationalisation des indicateurs de biodiversité européens (Streamlining European Biodiversity Indicators). Il émane de l'Agence Européenne de l'Environnement pour suivre l'état de la biodiversité en Europe (https://biodiversity.europa.eu/topics/sebi-indicators). Lancé en 2005, ce processus comprend 26 indicateurs (tous habitats confondus) censés évaluer les progrès faits pour atteindre l'objectif 2010 (désormais 2020) de stopper la perte de biodiversité en lien avec la Convention sur la Diversité Biologique (Convention on Biological Diversity, 1992). Dans ce système, deux indicateurs concernent explicitement la forêt (il s'agit des indicateurs 17 : stock et accroissement du bois sur pied et quantités exploitées ; et 18 : bois mort). Les autres sont communs à plusieurs milieux et ne concernent pas exclusivement la forêt (Figure 3).

Le second exemple est issu des conférences ministérielles spécifiques à la forêt (Strasbourg 1990, Helsinki 1993 et suivantes) qui ont émané de la conférence sur la diversité biologique, le processus pan-européen « Forest Europe » (anciennement Conférence Ministérielle pour la Protection des Forêts en Europe) a pour but d'évaluer le caractère durable de la gestion forestière. Il comprenait, en 2015, 5 indicateurs de politique générale, 12 indicateurs qualitatifs et 35 indicateurs quantitatifs (Forest Europe, 2015a). Les indicateurs quantitatifs sont regroupés en 6 critères de développement durable : 1. Ressources forestières ; 2. Santé et vitalité des forêts ; 3. Fonctions de production ; 4. Biodiversité ; 5. Fonctions de protection ; 6. Fonctions socio-économiques. Le critère 4 est spécifiquement dédié à la biodiversité et comprenait 9 indicateurs en 2015 (Forest Europe, 2015a). Outre le rapportage quinquennal sur l'état des forêts en Europe, un des objectifs de ce processus est de suivre l'état et la dynamique de la biodiversité forestière et de chercher à réduire les pressions qu'elle subit au travers de réponses institutionnelles et sociétales adaptées (Gabrielsen & Bosch, 2003).

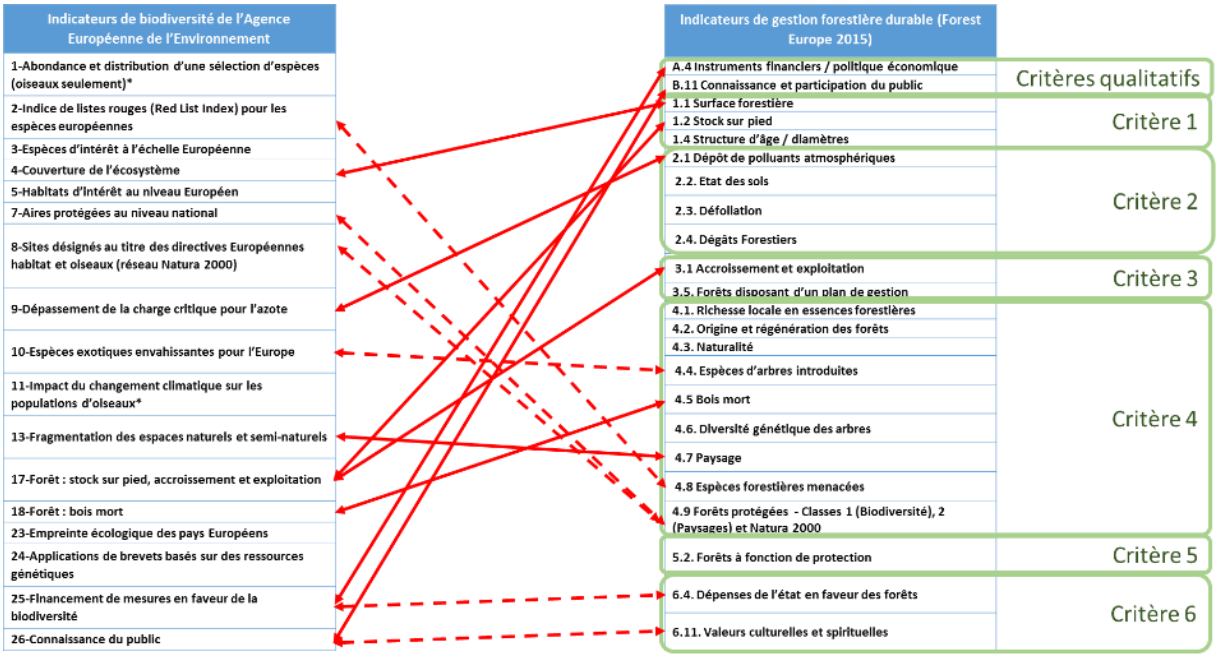


*Figure 3 : Correspondance entre les indicateurs de biodiversité européens applicables à la forêt (Agence Européenne de l'Environnement, à gauche), et les indicateurs européens de gestion forestière durable (répartis dans les critères de Forest Europe, à droite). Pour ces derniers, seuls les indicateurs ayant un lien supposé avec la biodiversité ont été figurés. Les liens en pointillés traduisent une correspondance partielle. *Un indicateur sur les populations d'oiseaux devrait être intégré dans le rapportage 2020 des indicateurs de gestion durable. D'après Lier et al. (2013).*

La Figure 3 compare les indicateurs de deux processus au travers du prisme des indicateurs Européens de biodiversité liés à la forêt. Cette comparaison succincte montre que :

- Si tous les indicateurs Européens de biodiversité ne concernent pas explicitement la forêt, une majorité (17/26) peuvent avoir une déclinaison forestière ;
- Tous les indicateurs Européens de biodiversité n'ont pas d'équivalents dans Forest Europe. Inversement, tous les indicateurs du critère 4 de biodiversité de Forest Europe ne se retrouvent pas dans les indicateurs européens (seulement 5/9) ;
- Enfin, tous les indicateurs de Forest Europe ayant un lien potentiel avec la biodiversité (qu'ils décrivent une pression, un état ou une réponse) ne se situent pas dans le critère 4 qui lui est dédié.

Plus généralement, les indicateurs utilisés dans ces deux processus sont de nature plutôt descriptive que normative (au sens de Heink & Kowarik, 2010a), même si leur caractère évaluatif ne semble jamais très éloigné – bien qu'assez peu explicité – dans la mesure où ils émanent d'initiatives avant tout politiques (notamment la Convention sur la Diversité Biologique, Feest, 2013). Cette lecture rapide met en évidence une partie des redondances et des lacunes de ces processus. Elle permet aussi d'introduire leurs limites.

1.3.2 Limites de ces indicateurs

En grande partie basés sur des données existantes – notamment celles des inventaires forestiers nationaux pour Forest Europe (Tomppo et al., 2010), au travers d'une approche résolument pragmatique (*cf.* Feest, 2013, pour les indicateurs de l'Agence Européenne de l'Environnement), les indicateurs utilisés dans ces deux processus couvrent assez mal la part de la biodiversité typiquement forestière (Gosselin et al., 2012; Paillet, 2017; Paillet et al., 2013). Par ailleurs, ces indicateurs sont principalement indirects, dans la mesure où ils utilisent des indices de structure et paysagers comme proxies de biodiversité, avec des liens parfois peu clairs :

(i) Le lien entre les deux indicateurs de l'Agence Européenne de l'Environnement dédiés à la forêt et la biodiversité est discutable. Au vu de l'absence de standardisation de la mesure du bois mort et de la corrélation statistique modérée avec la richesse totale d'organismes saproxyliques, notamment en forêt tempérée (voir Lassauce et al., 2011 pour les coléoptères et les champignons), sa pertinence en terme d'indicateur peut être légitimement remise en cause, tout au moins dans sa forme actuelle (Bouget, 2013). De même, le lien entre l'indicateur concernant le stock de bois sur pied, son accroissement et son exploitation et la biodiversité est équivoque et fondé sur un corpus théorique limité. Il est en effet peu interprétable sans plus de précisions dans la mesure où la réponse de la biodiversité peut varier fortement suivant les modalités d'exploitation mises en œuvre (sylviculture proche de la nature, coupes progressives, plantation…), les taxons étudiés et les échelles (*e.g.* Paillet et al., 2010) ;

(ii) Seuls deux indicateurs de Forest Europe (4.1. Richesse en espèces d'arbres, et 4.8. Espèces forestières menacées) sont des indicateurs taxonomiques (directs) de biodiversité, alors que six autres sont indirects (le cas des ressources génétiques est à part, car sa position en tant qu'indicateur de biodiversité est discutable, Lier et al., 2013).

De ce fait, ces processus, dépourvus d'un système de suivi taxonomique direct dédié (Gosselin et al., 2012; Paillet, 2017; Paillet et al., 2013), parviennent assez mal à rendre compte de l'état de la biodiversité et de la complétude des engagements à stopper son érosion (*e.g.* Feest, 2013). Pour les indicateurs de biodiversité existants, le niveau de preuve scientifique de leur lien effectif avec la biodiversité reste relativement faible (Gao et al., 2015). Ces difficultés ne sont pas spécifiques à ces processus internationaux, mais concernent également des initiatives nationales : (i) les indicateurs de gestion forestière durable, qui sont une déclinaison nationale de Forest Europe ; (ii) les indicateurs de

l'Observatoire National de la Biodiversité (http://indicateurs-biodiversite.naturefrance.fr) ; mais aussi (iii) des processus d'évaluation (*e.g.* état de conservation des habitats de la directive (https://inpn.mnhn.fr/programme/rapportage-directives-nature/presentation) et (iv) de certification forestière (https://www.pefc-france.org/, https://fr.fsc.org/fr-fr).

Ainsi, malgré des avancées récentes non négligeables (*e.g.* Lindenmayer et al., 2006; Smith et al., 2008), les études scientifiques permettant de documenter et mettre en œuvre de manière rigoureuse des indicateurs de gestion forestière durable – a fortiori de biodiversité – restent peu nombreuses (Angelstam et al., 2013; Barbier et al., 2009). Au final, malgré ces systèmes d'indicateurs, les choix de gestion et les orientations politiques liés à la biodiversité relèvent encore très souvent de « l'anecdote ou du mythe » plus que de la preuve scientifique (Sutherland et al., 2004) et la forêt n'échappe guère à la règle. Pour les indicateurs utilisés, le lien avec la biodiversité et leur robustesse semblent souvent assez mal documentés et peu fondés sur des données scientifiques.

Ce travail de thèse traite d'un indicateur indirect de biodiversité, c'est-à-dire d'un indicateur reposant sur le lien entre structure (et dans une moindre mesure la composition) de l'écosystème et biodiversité (Lindenmayer et al. 2000). Le cas d'étude choisi concerne les microhabitats des arbres comme descripteur de biodiversité (Heink & Kowarik, 2010b). Je propose une forme de validation scientifique (au sens de Niemeijer & de Groot, 2008) de cet indicateur potentiel au travers de trois aspects détaillés ci-dessous : ils sont d'ordre méthodologique (standardisation des relevés et biais observateurs), contextuel (facteurs d'influence à deux échelles) et corrélatif (lien avec la biodiversité de 3 taxons). La partie analytique de ce travail s'inscrit résolument dans la discipline scientifique de l'écologie, avec l'approche descriptive et statistique qui en découle. En effet, sur la base d'un seul indicateur potentiel, il semble difficile d'appliquer une analyse politique de sa mise en œuvre à des niveaux plus large. Cependant, le processus de validation dépasse le cadre disciplinaire du présent travail et certains aspects en seront discutés.

1.4. Modèle d'étude : cas des microhabitats

1.4.1 Que sont les microhabitats des arbres ?

Au sens large, le terme « microhabitat » englobe un ensemble de structures forestières de petites dimensions, généralement support d'une biodiversité particulière (espèces ou groupes d'espèces qui utilisent ce support pour se développer, nicher ou se nourrir, Tableau 1). Dans ce travail, le terme « microhabitat » (ou dendro-microhabitat, Larrieu, 2014) est restreint aux structures portées par les arbres sur pied, morts ou vivants (Michel & Winter, 2009; Vuidot et al., 2011; Winter & Möller, 2008). Ainsi, sous ce terme sont par exemple regroupées les cavités, les caractéristiques de l'écorce, ou les fentes, qui ont un rôle important pour de nombreux pans de biodiversité (Siitonen, 2012). Cette acception assez large est cependant relativement vague et ne constitue pas une définition claire et précise de l'ensemble des structures que recouvrent les microhabitats.

1.4.2 Rôle pour la biodiversité

D'un point de vue théorique, ils constituent une partie de la niche écologique d'un nombre important de taxons (Regnery et al., 2013a; Winter & Möller, 2008), avec un rôle fonctionnel parfois mieux décrit que d'autres éléments de structure (*e.g.* Gossner et al., 2016). Au regard de leur petite taille, les microhabitats semblent également présenter un rôle démesuré pour la biodiversité, ce qui rejoint la notion de « petite structure naturelle » récemment développée dans le numéro spécial du journal Biological Conservation (voir : Hunter et al., 2017). En effet, une grande diversité d'espèces et de groupes d'espèces sont liées pour tout ou partie de leur cycle de vie à un ou plusieurs microhabitats (Siitonen, 2012) : principalement des insectes, des arachnides, des gastéropodes, des oiseaux, certains

mammifères, amphibiens et reptiles, mais aussi des bryophytes, des champignons et des lichens. Ces groupes utilisent – et pour certains sont à l'origine – des microhabitats pour se nourrir, nicher et se reproduire. Certains microhabitats hébergent des groupes spécifiques, par exemple les dendrothelmes (cavités remplies d'eau de manière intermittente) présentent des assemblages d'espèces qu'on ne trouve pas dans d'autres milieux aquatiques (Dajoz, 2007 ; Gossner et al., 2016). Parce qu'ils sont portés par des entités biologiques – les arbres –, les microhabitats sont des structures dynamiques et en constante évolution qualifiées d'îlots de ressources éphémères par certains auteurs (« ephemeral ressource patches », Finn, 2001).

1.4.3 Un intérêt naturaliste et scientifique ancien récemment renouvelé

La littérature concernant les microhabitats est relativement ancienne et relève en premier lieu d'une connaissance naturaliste et experte des espèces liées à ces structures (voir la synthèse de Dajoz, 2007 pour les insectes, et les références citées dans ce livre). Loin d'être anecdotique, cette source de connaissance reste néanmoins très descriptive et appliquée à des objectifs de gestion en faveur de la biodiversité (*e.g.* Bull et al., 1997; Parks et al., 1997). Plus récemment, des approches en écologie se sont focalisées sur des types de microhabitats particuliers, et notamment sur les cavités qui sont de loin les objets les plus concernés par la littérature, *cf.* la synthèse de Remm and Lõhmus (2011) et, par exemple, les travaux de Cockle et al. (2011). Ces approches fournissent une connaissance disparate de certains taxons ou types de microhabitats. L'intérêt de synthétiser cette connaissance a émergé assez récemment sous la forme de typologies destinées à décrire ces structures, afin d'avoir un outil dédié à la prise en compte de la biodiversité dans la gestion forestière (Larrieu et al., 2012; Vuidot et al., 2011; Winter & Möller, 2008). Il en a résulté des études sur le lien entre listes de microhabitats d'une part, et caractéristiques des arbres (Larrieu & Cabanettes, 2012; Vuidot et al., 2011; Winter et al., 2015), de l'environnement ou de la gestion (Großmann et al., 2018; Larrieu et al., 2014a) et biodiversité (Bouget et al., 2014; Bouget et al., 2013; Regnery et al., 2013a; Winter & Möller, 2008) d'autre part. Par ailleurs, l'absence de standardisation des typologies ainsi que des méthodes de relevés fait que, malgré les initiatives récentes d'homogénéisation et de diffusion de standards (Kraus et al., 2016), la comparaison des données issues de différentes sources est pour le moment difficile (*cf.* néanmoins Larrieu et al., 2014b). Enfin, les tentatives d'établir le lien avec la biodiversité qui dépend potentiellement des microhabitats a jusqu'à présent été focalisée sur peu de taxons (*e.g.* Bouget et al., 2014; Bouget et al., 2013; Regnery et al., 2013a), alors que leur présence conditionne *a priori* une diversité multitaxonomique.

1.4.4 Les microhabitats, potentiels indicateurs de biodiversité

Des liens empiriques entre microhabitats et biodiversité ont été mis en évidence dans la littérature scientifique et naturaliste (*e.g.* Dajoz, 2007). Ils montrent un rôle potentiellement complémentaire à d'autres éléments de structure forestière traditionnellement utilisés comme indicateurs de biodiversité (*e.g.* bois mort, gros arbres). La question de l'utilisation des microhabitats comme indicateurs de biodiversité s'est ainsi assez rapidement posée (Regnery et al., 2013a; Vuidot et al., 2011; Winter & Möller, 2008). Leur facilité d'observation supposée, notamment par un public non expert (Regnery et al., 2013b) et la possibilité pour les gestionnaires d'avoir une influence directe sur leur état et leur dynamique, renforce l'intérêt qui leur est porté. Ainsi, les microhabitats semblent *a priori* remplir un certain nombre de conditions qui font d'eux de bons candidats-indicateurs de biodiversité.

Cependant, au regard des processus de validation « scientifique » d'indicateurs, un certain nombre de verrous persistent. Ils sont tout d'abord d'ordre méthodologique, à commencer par la standardisation des relevés et la quantification des biais potentiels qui peuvent les affecter. Ensuite, les facteurs qui influencent l'état et la dynamique des microhabitats restent méconnus, et ce aussi bien à l'échelle de l'arbre que de la parcelle forestière, ce qui ne permet qu'une prise en compte partielle – hors contexte – dans la gestion forestière. En particulier, peu d'études mentionnent les niveaux atteignables dans

des conditions d'évolution libre de la structure forestière (*i.e.* sur un gradient qui dépasse celui de l'exploitation forestière). Ces verrous sont enfin d'ordre analytique dans la mesure où peu d'études ont quantifié le lien entre indices de microhabitats basés sur des listes (richesse, abondance, diversité) et biodiversité multitaxonomique. La levée partielle de ces verrous constitue le cœur de mon travail de thèse et est à l'origine de sa problématique générale.

1.5. Problématique et hypothèses de travail

1.5.1 Réduire les incertitudes

L'établissement de procédures standardisées opérationnelles est un prérequis indissociable d'une démarche qualité associée à un recueil de données scientifiques (Allegrini et al., 2009; Ferretti, 2013). Ces procédures et protocoles garantissent la standardisation et la répétabilité des inventaires, avec un bruit statistique et une marge d'erreur faibles. Ils assurent le cas échéant la qualité d'un suivi spatial et temporel (Allegrini et al., 2009; Ferretti, 2013). L'établissement de standards est également une caractéristique des objets frontières (Trompette & Vinck, 2009; Turnhout, 2009) auxquels peuvent être rattachés les indicateurs, et par extension les microhabitats. Ces standards, en dehors d'assurer la qualité des données recueillies, permettent le dialogue entre les acteurs et les disciplines. Dans la mesure où les indicateurs de biodiversité sont avant tout un outil de gestion et d'évaluation, il parait nécessaire d'établir une typologie. C'est l'objet du Chapitre 2 de cette thèse, qui se compose de deux parties sous forme d'articles scientifiques et qui constitue l'apport méthodologique de ce travail.

Le premier article (Larrieu et al., 2018, Chap. 2, section 2.1) est issu d'un travail collaboratif basé sur un réseau d'experts et de scientifiques européens. L'intérêt soulevé par les microhabitats a donné lieu à l'établissement de plusieurs typologies partiellement discordantes, établies soit par des scientifiques (Larrieu & Cabanettes, 2012; Vuidot et al., 2011; Winter & Möller, 2008), soit par des gestionnaires (Bruciamacchie, 2005). Afin que la connaissance des microhabitats, des facteurs qui les influencent et du lien avec la biodiversité puissent progresser, il était nécessaire d'établir une typologie de référence. Le premier article propose une typologie morphologique basée sur le lien fonctionnel (établi ou supposé) entre microhabitats et diversité de plusieurs groupes d'espèces, avec une structure hiérarchique, adaptative et évolutive. L'article ne répond pas à des hypothèses spécifiques mais plutôt à une nécessité opérationnelle d'établir un référentiel typologique. Notons que ce travail de thèse n'échappe pas à l'écueil typologique puisque les publications présentées par la suite n'utilisent pas moins de trois typologies qui diffèrent substantiellement. Cependant, les regroupements effectués sont cohérents d'une partie à l'autre, de manière à ce que les résultats, notamment au niveau des types de microhabitats, restent comparables (Tableau 1).

Le second article (Paillet et al., 2015a, Chap. 2, section 2.2) porte sur la quantification de l'effet observateur sur les inventaires de microhabitats. L'effet observateur est une source de biais assez connue dans les inventaires basés sur l'observation et pourtant largement négligé dans les suivis, notamment de biodiversité (Archaux et al., 2006; Ferris & Humphrey, 1999). Réputés accessibles à des non spécialistes, les relevés de microhabitats sont potentiellement aussi sensibles que d'autres mesures et inventaires à l'effet observateur. Du fait de l'intérêt assez récent pour ces structures, aucune étude n'a encore cherché à évaluer l'influence des observateurs, de leur expérience et de la durée d'inventaire sur la qualité de l'observation. Au regard des études publiées sur d'autres types de mesures, l'hypothèse est que les caractéristiques des observateurs (identité, expérience) aussi bien que la durée consacrée à l'inventaire ont des effets forts sur la précision des inventaires, en rapport avec un inventaire de référence (consensus). Ce travail repose sur une expérimentation conduite en forêt de Fontainebleau, sur deux placettes de 0.5ha situées dans une des réserves intégrales historiques (>150 ans sans exploitation forestière) qui ont été cartographiées pour l'occasion. Il a mobilisé 14 observateurs d'origine et d'expériences diverses.

Larrieu et al. (2018)			Vuidot et al. (2011), d'après Winter et al. (2005)	Typologie ENGREF
Forme	**Groupe**	**Type**		
Cavités s.l.	Loges de pic	Loge de petite taille (<4cm)	Cavité de pic	Loge
		Loge de taille moyenne(4-7cm)		
		Loge de grande taille (>10cm)		
		"Flute" de cavités (> 3 en ligne)		
	Cavités à terreau	Cavité à terreau de pied	Grande cavité de pied	Cavité
		Cavité à terreau de tronc	Cavité à terreau de tronc	
		Cavité à terreau semi-ouverte	Cavité d'origine naturelle (carie)	
		Cavité à terreau (cheminée) + contact sol		
		Cavité à terreau (cheminée) sans contact sol		
		Branche creuse		
	Galeries d'insectes	Orifices et galeries d'insectes		
	Concavités	Dendrothelme		
		Trou de nourrissage de pic		Attaque de pic (pour consommation)
		Concavité à fond dur de tronc		
		Concavité racinaire		
Blessures et bois apparents	Aubier apparent	Bois sans écorce	Absence d'écorce ou blessure récente	Blessure
		Blessure due au feu		
		Ecorce décollée (abri)	Ecorce déhiscente (2 types : avec et sans pourriture)	Ecorce déhiscente
		Ecorce décollée (poche)		
	Aubier et bois de coeur apparents	Cime brisée	Tête cassée	Tête cassée ou sèche
		Bris de charpentière	Fourche cassée	
		Fente		Fente
		Fente causée par la foudre	Fente causée par la foudre	
		Fente au niveau de la fourche		
Bois mort dans le houppier	Bois mort dans le houppier	Branches mortes	Branches mortes (3 classes de proportion du houppier : 10-25, 25-50 et >50%)	Branches mortes (3 classes de taille : 5-10, 10-30,>30cm)
		Cime morte	Squelette de houppier (arbres morts uniquement)	Ensemble du squelette du houppier
		Vestige de charpentière brisée		
Excroissances	Agglomérations de gourmands ou de rameaux	Balai de sorcière	Balai de sorcière	
		Gourmands / Brogne		
	Loupes et chancres	Loupe		
		Chancre	Chancre	
Sporophores de champignons et Myxomycètes	Sporophores de champignons perennes	Polypore pérenne	Carpophore de polypore (3 classes : 1-2, >3 carpophores, en cascade)	Champignon
	Sporophores de champignons éphémères et Myxomycètes	Polypore annuel		
		Agaricale charnu		
		Pyrénomycète		
		Myxomycète		
Structures épiphytiques, épixyliques ou parasites	Plantes et lichens épiphytiques ou parasites	Bryophytes	Bryophytes	Mousse
		Lichens foliacés ou fruticuleux		Lichen
		Lierre ou lianes	Lierre	Lierre
		Fougères		
		Gui		
	Nids	Nid de Vertébré		
		Nid d'invertébré		
	Microsols	Microsol d'écorce		Pourriture (?)
		Microsol du houppier		Fourche avec terreau
Exsudats	Exsudats	Coulée de sève	Eclatement noir avec sève ou résine + Coulée de sève ou résine (2 types : faible, forte)	
		Coulée abondante de résine		
			Tronc déchiqueté	
7 formes	**15 groupes**	**47 types**	**26 types**	**17 types***

*Tableau 1 : Comparaison des différentes typologies utilisées dans ce travail. *6 autres types de cette typologie se réfèrent à des caractéristiques individuelles d'arbres (e.g. tortuosité) et ne constituent pas des microhabitats au sens de Larrieu et al. (2018).*

1.5.2 Mieux comprendre les facteurs d'influence des microhabitats à différentes échelles

Qualifiée de robustesse ou de portabilité, la capacité d'un indicateur à conserver le lien avec son *indicandum* dans diverses situations est un autre prérequis de validation (Niemeijer & de Groot, 2008). Il est donc nécessaire de comprendre quels sont les facteurs qui influencent, en premier lieu, l'indicateur potentiel, dans une optique d'applicabilité à la gestion et d'une contextualisation des niveaux atteignables en l'absence de gestion, par exemple. Dans le cas des microhabitats, les facteurs d'influence peuvent intervenir à au moins deux échelles : celle de l'arbre porteur de microhabitats et celle de la parcelle forestière, notamment en fonction du mode de gestion qui lui est appliqué. L'originalité de cette approche est de travailler sur un gradient de gestion forestière comprenant une part importante de peuplements peu ou pas exploités (réserves forestières intégrales). Ce gradient de maturité élargi permet de discuter des références pour la gestion forestière, en particulier des niveaux atteints en cas d'arrêt d'exploitation forestière. L'analyse de ces facteurs est l'objet du Chapitre 3 de la thèse et comprend deux articles.

Le troisième article de cette thèse (Paillet et al., preprint, Chap. 3, section 3.1) analyse l'influence des caractéristiques individuelles de l'arbre sur la richesse et l'occurrence des microhabitats. Sur la base des travaux antérieurs (Larrieu & Cabanettes, 2012; Regnery et al., 2013b; Vuidot et al., 2011), les hypothèses sont que les indices de microhabitats au niveau arbre varient avec l'essence considérée (avec notamment plus de microhabitats sur les feuillus que sur les résineux), le diamètre (plus les arbres sont gros plus ils portent de microhabitats) et la vitalité (les arbres morts portent plus de microhabitats que les vivants). En comparaison avec les études précédentes, l'originalité de ce travail a reposé sur la capacité d'analyser les interactions entre ces facteurs d'influence et d'intégrer des variables abiotiques (altitude, température, pluviométrie). Cette analyse a été rendue possible par l'utilisation d'un jeu de données issu de relevés effectués dans les réserves forestières à l'échelle nationale. Cette base de données comprenait initialement plus de 8000 placettes pour plus de 100 000 arbres, de laquelle un échantillon analysable d'environ 22000 arbres répartis sur 43 sites à l'échelle nationale a été extrait.

Le quatrième article (Paillet et al., 2017, Chap. 3, section 3.2) compare les densités observées de microhabitats entre zones forestières en réserve intégrale et zones exploitées pour la production de bois. Ce travail cherche à valider plusieurs hypothèses :

(i) Les densités de microhabitats sont plus fortes en réserves intégrales qu'en zone exploitée ;
(ii) Les densités plus fortes observées en zone non exploitée sont liées avant tout à l'abondance supérieure d'arbres porteurs (gros arbres vivants et arbres morts) en réserve, et ce malgré leur faible contribution à la densité totale ;
(iii) De même, l'abondance des microhabitats individuels (types) diffère entre forêt exploitée et non exploitée, certains types présentant des densités plus fortes en forêts exploitées et d'autres (plus nombreux) en forêt non exploitée ;
(iv) Les densités de microhabitats liées à l'arrêt d'exploitation, et donc l'abondance totale de microhabitats, croit avec la date depuis la dernière exploitation de bois (et inversement pour ceux liés à l'exploitation de bois).

Ces analyses reposent sur un plan d'échantillonnage comprenant 222 placettes forestières situées dans 17 sites répartis sur toute la France et qui comparent zones en réserve intégrale et zones exploitées pour la production de bois. Ce jeu de données est issu du projet « Gestion forestière, Naturalité et Biodiversité » associant Irstea, l'Office National des Forêts et les Réserves Naturelles de France (www.gnb.irstea.fr).

1.5.3 Quantifier le lien avec la biodiversité

Le lien entre microhabitats et biodiversité repose essentiellement sur des bases empiriques expertes et naturalistes (Larrieu et al., 2018). Le lien quantitatif basé sur des approches statistiques solides est plus rare, notamment dans un contexte multitaxonomique. La quantification de ce lien est pourtant un des prérequis essentiels de la validation d'un indicateur de biodiversité (*cf.* Section 1.1.2.4). D'autre part, on peut supposer un lien causal entre mode de gestion (notamment mise en réserve intégrale, *i.e.* arrêt de l'exploitation de bois), arbres porteurs de microhabitats (vivants ou morts, notamment ceux de forts diamètres) et microhabitats. L'arrêt d'exploitation, en favorisant le développement d'éléments structuraux caractéristiques de vieilles forêts (Bauhus et al., 2009; Paillet et al., 2015b; Vandekerkhove et al., 2009), aurait un effet positif sur la densité et la diversité de microhabitats. Il pourrait également en découler un effet positif sur la biodiversité. Les microhabitats seraient alors vus comme des médiateurs de la mise en réserve et de l'augmentation des structures typique des vieilles forêts sur la biodiversité.

Ce sont ces hypothèses que j'ai testées dans l'article présenté dans le Chapitre 4 (Paillet et al., in press). Le cadre statistique formel des équations structurelles a été utilisé pour étudier le lien causal potentiel entre arrêt d'exploitation, éléments de structure forestière de grandes dimensions (gros arbres vivants et morts), microhabitats et diversité de trois groupes taxonomiques : chauves-souris, oiseaux et coléoptères saproxyliques. Cet article vient compléter au travers d'un exemple multitaxonomique à large échelle la synthèse de Larrieu et al. (2018, Chap. 2, section 2.1). Il repose sur une partie du jeu de données utilisé pour l'analyse des facteurs d'influence sur les microhabitats au niveau de la parcelle forestière (Chap. 3, section 3.2), complété par des relevés taxonomiques.

Le Tableau 2 résume les principales questions et hypothèses de cette thèse et les jeux de données mobilisés.

Chapitre	Questions	Hypothèses	Données mobilisées	Article
Chapitre 2	1. Comment établir une liste de référence pour l'inventaire des microhabitats en Europe ?	Pas d'hypothèse spécifique	Bibliographie et expertise	Larrieu et al. Ecol. Ind. 2018
	2. Les inventaires de microhabitats sont-ils soumis à un effet observateur ?	Effets forts des caractéristiques des observateurs (identité, expérience, familiarité), et de la durée sur la précision des inventaires	2 placettes de 0.5ha en forêt de Fontainebleau (106 arbres) 14 observateurs	Paillet et al. Ecol. Ind. 2015
Chapitre 3	Quels sont les facteurs d'influence des microhabitats ?	<u>A l'échelle de l'arbre</u> : Effet positif du diamètre Plus de microhabitats sur arbres morts Différence de réponse en fonction de l'essence Différence de réponse en fonction des conditions biogéoclimatiques	2783 placettes réparties sur 43 sites à échelle nationale (22000 arbres)	Paillet et al. preprint
		<u>A l'échelle de la parcelle forestière</u> : Densités de microhabitats plus fortes en réserves intégrales qu'en zone exploitée ; Densités supérieures en réserve liées à l'abondance de gros arbres vivants et arbres morts ; Différence d'abondance des microhabitats individuels (types) entre forêt exploitée et non exploitée ; Augmentation des densités de microhabitats avec la date depuis la dernière coupe.	222 placettes comparant forêt exploitées et non exploitées, réparties sur 17 sites à l'échelle nationale	Paillet et al. For. Ecol. Man. 2017
Chapitre 4	Quel lien entre microhabitats et biodiversité de 3 taxons : chauves-souris, oiseaux et coléoptères saproxyliques ?	<u>Existence d'un lien causal positif entre</u> : L'arrêt d'exploitation ; Les caractéristiques de vieilles forêts ; La densité et la diversité des microhabitats ; La biodiversité des 3 groupes taxonomiques.	213 placettes comparant forêt exploitées et non exploitées, réparties sur 15 sites à l'échelle nationale	Paillet et al. J. App. Ecol. 2018

Tableau 2 : Résumé des questions principales, des hypothèses, des données mobilisées et des articles correspondants dans ce travail de thèse.

Chapitre 2 - Réduire les incertitudes : apports méthodologiques

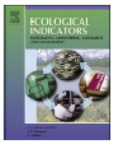
2.1. Définir un référentiel standardisé : “Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization” – Larrieu et al. Ecol. Ind. (2018)

Ecological Indicators 84 (2018) 194–207

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



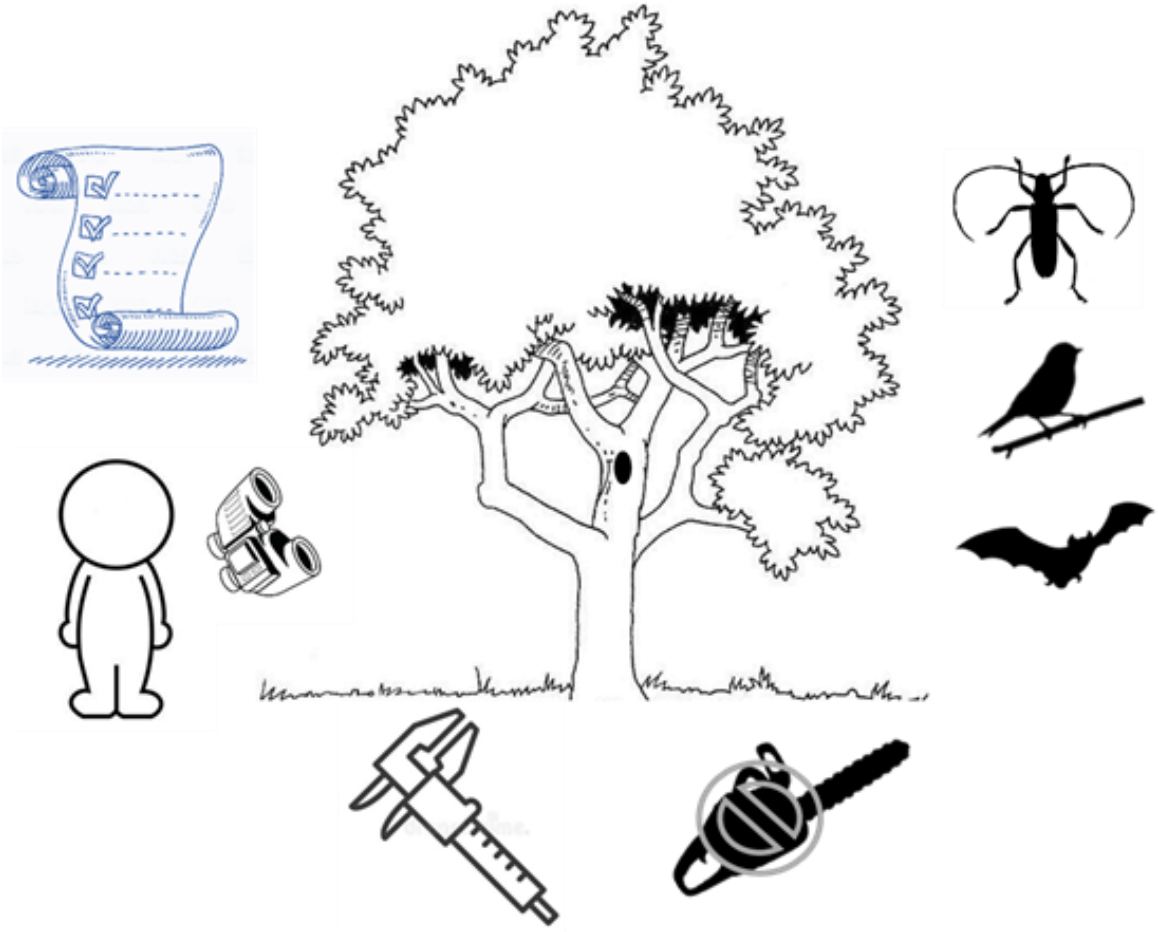
Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization

Laurent Larrieu[a,b,*,1], Yoan Paillet[c,1], Susanne Winter[d,1], Rita Bütler[e], Daniel Kraus[f], Frank Krumm[g], Thibault Lachat[g,h], Alexa K. Michel[i], Baptiste Regnery[j,k], Kris Vandekerkhove[l]

Résumé

Les microhabitats des arbres sont reconnnus comme des substrats et des structures importantes pour la biodiversité, à la fois dans les forêts de production et les forêts protégées. A ce titre, ils recoivent une attention croissante par les gestionnaires, les conservateurs d’espaces naturels et les chercheurs. L’inventaire des microhabitats des arbres a récemment suscité un intérêt, dans la mesure où ils constituent un indicateur indirect pour les espèces spécialistes qui les utilisent comme substrat ou habitat, au moins pour une partie de leur cycle de vie. Cependant, il existe encore une large acception de ce qui constitue précisément un microhabitat et de la façon de les relever sur le terrain.

Dans le but d’harmoniser les futurs inventaires de microhabitats des arbres, nous proposons une définition et une typologie des types de microhabitats portés par des arbres vivants et morts debouts, en forêt européenne tempérée et méditerranéenne. Notre but est de fournir aux utilisateurs des définitions qui permettent une détermination univoque des microhabitats. Notre typologie comprend sept formes de base prenant en compte des caractéristiques morphologiques et le lien avec la biodiversité : (i) les cavités au sens large ; (ii) les blessures et le bois apparent ; (iii) le bois mort du houppier ; (iv) les excoissances ; (v) les carpophores de champignons saproxyliques et assimilés ; (vi) les structures épiphytes et epixyliques ; et (vii) les exsudats. Cette typologie est ensuite structurée hierarchiquement en 15 groupes et 47 types, ce qui permet une utilisation pour différentes applications. La typologie, accompagnée d’un guide pour des inventaires standardisés, représente un outil de référence qui permet la comparaison des données de microhabitats entre différentes régions, types forestiers et essences, et devrait améliorer significativement la fiabilité des relevés de microhabitats. Elle fournit une base pour compiler de telles données et pourrait contribuer aux rapportages et à l’évaluation de la valeur de conservation des forêts. Au final, notre travail met en évidence la nécessité d’entreprendre des recherches complémentaires sur les microhabitats de manière à mieux comprendre leur dynamique et leur lien avec la biodiversité, et ainsi inclure pleinement leur suivi dans la gestion forestière courante.



Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization

Laurent Larrieu*[1,2,a], Yoan Paillet[3,a], Susanne Winter[4,a], Rita Bütler[5], Daniel Kraus[6], Frank Krumm[7], Thibault Lachat[8,9], Alexa K. Michel[10], Baptiste Regnery[11,12], Kris Vandekerkhove[13]
*Corresponding author, [a]These authors contributed equally

[1] INRA, UMR1201 DYNAFOR, Chemin de Borde Rouge, Auzeville, CS 52627, 31326 Castanet Tolosan Cedex, France, Tel: +33 5 61 28 54 92; Fax: +33 5 61 28 54 11, e-mail: laurent.larrieu@inra.fr
[2] CRPF-Occitanie, 7 chemin de la Lacade, 31320 Auzeville Tolosane, France, e-mail: laurent.larrieu@crpf.fr
[3] Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France, Tel.: +33 238950343, Fax: +33 28950359, e-mail: yoan.paillet@irstea.fr
[4] WWF World Wide Fund for Nature Germany, Reinhardtstraße 18, 10117 Berlin, Germany. Tel.: +49 30 311 777 235, Fax +49 30 311 777 199, e-mail: susanne.winter@wwf.de
[5] Swiss Federal Research Institute WSL, EPFL, Bât. GR Station 2, ECOS, 1015 Lausanne – Ecublens, Switzerland, e-mail: rita.buetler@wsl.ch
[6] Chair of Silviculture, University of Freiburg, Tennenbacherstr. 4, 79085 Freiburg im Breisgau, Germany, Tel.: +49 761 203-3678, e-mail: daniel.kraus@waldbau.uni-freiburg.de
[7] Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, email: frank.krumm@wsl.ch
[8] Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland, Tel.: +41 44 7392 309, Fax +41 44 7392 215, e-mail: thibault.lachat@wsl.ch
[9] Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences HAFL, Länggasse 85, 3052 Zollikofen, Tel.: +41 31 910 21 42, thibault.lachat@bfh.ch
[10] Thünen Institute of Forest Ecosystems, A.-Möller-Str. 1, Haus 41/42, 16225 Eberswalde, Germany, Tel.: +49 3334 3820-367, Fax +49 3334 3820-354, e-mail: alexa.michel@thuenen.de
[11] Muséum national d'Histoire naturelle, Service du Patrimoine Naturel, 4, avenue du Petit château 91800 Brunoy, France
[12] Observatoire Régional de l'Environnement Poitou-Charentes, Téléport 4 Antarès B.P. 50163, 86962 Futuroscope Chasseneuil Cedex, France. Tel.: +33 (0) 5 49 49 71 17, Fax : +33 (0) 5 49 49 61 01, email : regnery@observatoire-environnement.org
[13] Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium. Tel.: +32-54-437128, Fax : +32-54-436160, e-mail: kris.vandekerkhove@inbo.be

Abstract

Tree **re**lated **M**icrohabitats (hereafter TreMs) have been widely recognized as important substrates and structures for biodiversity in both commercial and protected forests and are receiving increasing attention in management, conservation and research. How to record TreMs in forest inventories is a question of recent interest since TreMs represent potential indirect indicators for the specialized species that use them as substrates or habitat at least for a part of their life-cycle. However, there is a wide range of differeing interpretations as to what exactly constitutes a TreM and what specific features should be surveyed in the field.

In an attempt to harmonize future TreM inventories, we propose a definition and a typology of TreM types borne by living and dead standing trees in temperate and Mediterranean forests in Europe. Our aim is to provide users with definitions which make unequivocal TreM determination possible. Our typology is structured around seven basic forms according to morphological characteristics and biodiversity relevance: i) cavities *lato sensu* ii) tree injuries and exposed wood, iii) crown deadwood, iv) excrescences, v) fruiting bodies of saproxylic fungi and fungi-like organisms, vi) epiphytic and epixylic structures, and vii) exudates. The typology is then further detailed into 15 groups and 47 types with a hierarchical structure allowing the typology to be used for different purposes. The typology, along with guidelines for standardized recording we propose, is an unprecedented reference tool to make data on TreMs comparable across different regions, forest types and tree species, and should greatly improve the reliability of TreM monitoring. It provides the basis for compiling these data and may help to improve the reliability of reporting and evaluation of the conservation value of forests. Finally, our work emphasizes the need for further research on TreMs to better understand their dynamics and their link with biodiversity in order to more fully integrate TreM monitoring into forest management.

Keywords: Biodiversity conservation, integrative forest management, monitoring, forest inventory, tree structure, wildlife habitat

Introduction

Over the last decades, biodiversity conservation has become an increasingly important management objective in multi-purpose forests (Hunter, 1999; Kraus and Krumm, 2013). However, despite large-scale forest initiatives (Convention on Biological Diversity, 1992; European Environmental Agency, 2008; Forest Europe, 2015), monitoring forest biodiversity or structural heterogeneity remains a challenge (Lindenmayer et al., 2006). In conventional forest inventories, direct biodiversity monitoring is often limited to only one, or a few, species groups because reliable records of biota are expensive and time-consuming and require taxonomic experts for inventory and interpretation (Winter et al., 2008). In addition, no taxon has been firmly identified as a relevant surrogate for all the other taxa yet (Wolters et al., 2006). Since total biodiversity cannot be measured due to its complexity, indirect methods have been developed, especially for species diversity (Larsson, 2001; Lindenmayer et al., 2000). Both management and nature conservation in forests focus mainly on general forest structure characteristics that are assumed to be essential for biodiversity and that can be influenced by forest management (Chirici et al., 2012; Winter et al., 2014). These characteristics include horizontal and vertical forest structure, tree species composition, tree age, tree diameter distribution, tree regeneration, and deadwood quantities and qualities. Efforts to include structurally based biodiversity indicators have notably relied on National Forest Inventory data (Food and Agriculture Organization, 2015; Forest Europe, 2015).

Emphasis has been put on biodiversity-related structures such as deadwood (*e.g.* Stokland et al., 2012) for which thresholds (Müller and Bütler, 2010) and references have been published (*e.g.* Christensen et al., 2005; Paillet et al., 2015b; Vandekerkhove et al., 2009). For example, deadwood volume has been used as a structural indicator for forest biodiversity monitoring in most European forest inventory protocols during the last two decades (Tomppo et al., 2010). Clear definitions and survey methods for assessing deadwood allow comparative studies (*e.g.* Christensen et al., 2005; Vandekerkhove et al., 2009), inventories and analyses to be carried out in a harmonized way (Rondeux et al., 2012).

In the quest for scientifically-based indirect structure indicators (Larsson, 2001), tree related microhabitats (hereafter refered to as TreMs) have recently gained attention in research and management (*e.g.* Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Regnery et al., 2013b; Siitonen, 2012; Vuidot et al., 2011; Winter et al., 2015b; Winter and Möller, 2008). Many studies focus on individual types, mainly cavities (*e.g.* Carvalho et al., 2014; Gouix and Brustel, 2012; Ranius et al., 2009; Remm and Lõhmus, 2011; Saunders et al., 2014). Among the authors who have studied several TreM types simultaneously (*e.g.* Kraus et al., 2016; Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Michel and Winter, 2009; Paillet et al., 2017; Vuidot et al., 2011; Winter and Möller, 2008), the definitions and lists used and the observation protocols applied generally differ. There are considerable variations among interpretations of what exactly a TreM is and which features should be recorded in the field. As a consequence, the results from different studies are hardly comparable, despite the harmonizing efforts of Larrieu et al. (2014b) and Winter et al. (2015b). Clear definitions as well as a standardized list and methodology are now needed to make it possible to compare studies focusing on the role of TreMs for biodiversity at the stand scale and to promote TreMs as biodiversity indicators in large-scale monitoring efforts.

Our first aim is to provide a clear definition of a TreM. Secondly, we propose a TreM typology with strong morphological and biodiversity relevance. Thanks to the hierarchical structure of our typology, it can be used by both researchers and forest managers; for example, as a tool to identify and conserve habitat trees in managed forests. We also provide guidelines for recording methods and required measurements to serve as a baseline for common application in monitoring, research and teaching. Finally, we discuss the relevance of the proposed typology and propose research perspectives in order to fill in the gaps in the current knowledge of TreMs. In particular, we emphasize the need to better understand TreM dynamics, relative to the specific forest context, and the link between specific TreMs and biodiversity.

1. Tree related Microhabitats: a definition based on their functional role for biodiversity

2.1. Definition

We define a Tree related Microhabitat (TreM) as a distinct, well delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrates or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed. TreMs are specific above-ground tree morphological singularities that are not to be found on every tree. TreMs encompass both tree-originating modifications caused by biotic and abiotic impacts, such as intrusions, lesions and breakages, which expose sap and heartwood and initialize outgrowth structures and wood decay (saproxylic TreM), as well as elements of external origin that are physically linked to the tree (epixylic TreM).

Although morphological singularities may also be observed on lying deadwood or roots, TreM are explicitly restricted to above-ground structures on standing trees, in order to avoid a too wide scope. Thus, we have deliberately excluded features of lying deadwood such as root plates, pits and mounds and particular wood decay structures. We also exclude generic tree species-specific characteristics, such as rough bark on oak or larch, acid or alkaline bark conditions, as well as peculiar tree growth forms (such as crooked, skewed or rotated trunks, low horizontal branching), resulting from specific abiotic conditions or haphazard growth.

2.2. Substrates and microclimates associated with TreMs

TreMs provide specific conditions, notably microclimatic conditions and substrates, where specialized taxa shelter, forage or breed. Therefore, there is a functional link between TreMs and species, ecological groups or guilds. In other words, TreMs constitute very small-scale habitat (or part of habitat) for associated and specialized species or species assemblages. TreMs thereby strongly contribute to the internal heterogeneity of forest stands. We classified the TreMs into 15 main microhabitat groups according to 12 substrates and four microclimatic conditions they provide (Tableau 3). The rarest substrates occurring in our typology are charred wood (from fire or lightning injuries), hyphal structures (on fungi conks), epixylic materials and supporting structures (such as nests). Other substrates are more common (*e.g.* exposed sap- and heartwood). Twelve out of fifteen TreMs supply buffered microclimates (mainly cavities) while one provides temporary water bodies (dendrotelm). Eight TreM groups provide potentially drier conditions than the surrounding microclimate, while seven TreM groups support higher humidity. Some TreMs, such as rot-holes, can offer either dry or wet microclimatic conditions depending on the time of the year: during rainy periods, such cavities offer a dry shelter, whereas during dry periods they still offer a relatively moist habitat.

Tableau 3 : Substrate types and microclimatic conditions associated with specific tree-related microhabitat (TreM) groups in European temperate and Mediterranean forests. X: feature systematically exhibited; (X): feature not systematically exhibited; [1]Mould consists of decayed wood commonly mixed with animal detritus; [2]Soil humus mixes organic and mineral components; [3]Organic humus consists of leaves, twigs, bryophytes, detritus, etc.; [4]Supporting structure is additional tree biomass not originating from regular tree growth.

	Substrate type											**Supporting structure[4]**	**Microclimatic conditions**			
TreM Groups	**Sapwood**	**Heartwood**	**Mould[1]**	**Soil humus[2]**	**Organic humus[3]**	**Animal detritus**	**Sap**	**Resin**	**Epixylic material**	**Hyphal structure**	**Charred wood**		**Buffered microclimate**	**Dry condition**	**Wet condition**	**Temporary water body**
Woodpecker breeding cavities		x	(x)		(x)	x	(x)	(x)					x	x		
Rot holes (containing mould)		x	x	(x)	(x)	x							x	(x)	(x)	
Insect galleries		x				(x)							x	x		
Concavities		x	(x)		(x)	(x)								(x)	(x)	(x)
Exposed sapwood only	x		(x)				(x)	(x)			(x)			(x)	(x)	
Exposed sapwood and heartwood	x	x					(x)	(x)			(x)		(x)	x	(x)	
Crown deadwood	(x)	(x)					(x)	(x)						(x)		
Twig tangles												x				
Burrs and cankers	(x)											x				
Perennial fungal fruiting bodies										x			x			
Ephemeral fungal fruiting bodies and slime moulds										(x)						
Epiphytic crypto- and phanerogams									x				(x)		(x)	
Nests						x			x				(x)	(x)	(x)	
Microsoil				x	x	(x)									x	
Exudates							(x)	(x)							x	

2.3. Biodiversity associated with TreMs

TreMs are patchy substrates that evolve constantly; they can therefore be considered as “ephemeral resource patches” (as defined by Finn, 2001). They are used by a wide variety of animals, plants and fungi, during at least a part of their life-cycle. Based on the literature (Annexe 1) and the authors’ expertise, we have selected nine broad taxonomic groups which use TreMs: insects, arachnids, gastropods, birds, mammals, amphibians and reptiles, bryophytes, fungi, lichens (Tableau 4). This supporting information does not aim to be exhaustive, but illustrates both the diversity and specificity of TreM-dwelling assemblages, some species being exclusively linked to certain TreM types (see *e.g.* Dajoz, 2007 for dendrotelm-dwelling species).

Arthropods are by far the main known users of TreMs with a large range of taxa concerned (see *e.g.* Dajoz, 2007; Stokland et al., 2012). These include the following insect orders: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera; and, to a lesser extent, other arthropods such as Collembola and Acari. Vertebrates are also prominent users of TreMs. TreMs also provide very important substrates and colonization entries for wood decaying fungi. However, the number of TreM specialized bryophytes and lichens is limited (Jahns, 1989).

The relationship at the TreM scale between cavity types such as woodpecker breeding cavities, mould cavities or dendrotelms, and the species communities they host is relatively well known and documented (*e.g.* Gossner et al., 2016; Gouix and Brustel, 2012; Martin and Eadie, 1999; Ranius, 2002). However, knowledge of the communities hosted by other TreM types such as bark microsoil is relatively scarce (Halama et al., 2014).

*Tableau 4 : Link between tree-related microhabitats (TreMs) groups and biodiversity in European temperate and Mediterranean forests. "x" indicates that several species of the taxonomic group occur; these species are not necessarily strictly associated with the TreM group. « * » (used for Hymenoptera only) indicates that TreM-associated species are mostly parasitoids. See Annexe 1 for supporting references and the list of the experts consulted.*

	Invertebrates									**Vertebrates**					**Bryophytes**	**Fungi**	**Lichens**
	Insects						**Arachnids**		**Gastropods**	**Birds**	**Mammals**			**Amphibians & Reptiles**			
TreM groups	**Coleoptera**	**Diptera**	**Hemiptera**	**Hymenoptera**	**Lepidoptera**	**Collembola**	**Mites**	**Aranea, & Pseudoscorpionida**			**Rodents**	**Bats**	**Carnivores**				
Woodpecker breeding cavities	x	x		x*	x		x	x		x	x	x	x			x	
Rot-holes (containing mould)	x	x		x*		x	x	x	x	x	x	x	x	x	x	x	x
Insect galleries	x	x		x*			x	x				x				x	
Concavities	x	x		x*				x		x	x		x	x	x	x	
Exposed sapwood only	x			x	x				x	x		x				x	
Exposed sapwood and heartwood	x	x						x	x	x		x				x	x
Crown deadwood	x	x		x			x	x		x						x	x
Twig tangles								x		x							
Burrs and cankers					x										x	x	
Perennial fungal fruiting bodies	x	x	x	x*	x	x	x		x						x	x	
Ephemeral fungal fruiting bodies and slime moulds	x	x	x		x	x	x									x	
Epiphytic crypto- and phanerogams	x	x		x	x		x	x	x	x	x		x			x	
Nests	x	x			x		x	x		x	x		x			x	
Microsoil		x				x	x								x	x	
Exudates	x	x		x												x	

3. TreM hierarchical typology and protocol guidelines

3.1. Hierarchical typology

Following Larrieu (2016), we adopted a hierarchical approach to build our typology. We first identified seven general forms that share the same physiognomy and functional characteristics. Then, these forms were subdivided into fifteen more specific groups which can be further assigned to 47 distinct types based on morphological characteristics and biodiversity relevance (Tableau 5):

1. **Cavities** *lato sensu* are basically holes or shelters formed in the wood either by cavity builders (*e.g.* woodpeckers, saproxylic insects), decay processes (rot hole), morphological particularities on the trunk or collar (*e.g.* dendrotelms in forks or root-buttress shelters). They provide buffered climatic conditions and nesting sites for a wide array of species, from arthropods to large mammals. They can be subdivided into cavities *stricto sensu* in which the entrance is smaller than its interior diameter, and galleries and concavities if the entrance is of the same or greater width than the interior. This general form is sub-divided into four groups and 15 TreM types.

2. **Injuries** expose sapwood and sometimes also heartwood and create access for colonizing taxa. They are mainly created by mechanical impacts such as trunk or crown breakage from wind, ice or snow, but may also be caused by lightning strikes and frost, and occasionally by forest fires. They encompass two TreM groups and nine types. Exposed wood and injuries may evolve to rot holes over time if the tree is not able to seal the wound.

3. **Crown deadwood** consists of dead branches in general occurring at the top of the tree; this often provides open xero-thermophilous conditions due to the location in the canopy. Crown deadwood may also take the form of large broken branches where a thick dead branch section still remains. Dead tree tops, generally sun-lit, expose the heartwood and offer a transition between the living tree and dead wood. This form contains one TreM group and three types.

4. **Excrescences** are mainly caused by reactive growth to an increase in light availability or to a parasitic or microbial intrusion where the tree creates specific structures to isolate the pathogen (*e.g.* canker, burr). Excrescences are comprised of two TreM groups and four types.

5. **Fungal fruiting bodies and slime moulds** are the visible part of saproxylic fungi (or fungi-like organisms such as Myxomycetes) and are classified as perennial or ephemeral (lasting less than a year) structures. There are two TreM groups and five types in this general form.

6. **Epiphytic and epixylic structures** encompass a wide variety of structures in which the tree is merely the physical support on which the TreM grows or is located. These structures include different organisms growing on trees (cryptogams and phanerogams), vertebrate or invertebrate nests and also “perched” microsoils (developed from organic material such as leaves, bark, decaying bryophytes, etc.) either on trunk bark, at fork intersections or on a flat area within the crown. This general form is sub-divided into three TreM groups and nine types.

7. **Exudates** are sap runs or heavy resinosis and emcompass one TreM group and two types.

For each TreM type, we provide a definition (Tableau 6) and an illustration (Tableau 7) to facilitate correct field identification. For each type, we define a minimum threshold size for recording and monitoring purposes. These thresholds are based on biological features whenever possible (*e.g.* the size of the woodpecker species that builds a given type of cavity, Tableau 4), or a pragmatic approach was taken to allow for standardized inventories and reduce observer effect and observation time.

The classification into general forms (n=7), TreM groups (n=15) and TreM types (n=47) provides three hierarchical aggregation levels (grains) to be used differently depending on the aim of a given study, inventory or monitoring process. For example, the general form level can easily be applied for quickscans and for selecting habitat trees during tree marking and felling in managed forests; however, this grain is not fine enough for detailed monitoring. Thanks to the hierarchical structure, inventories

with a finer grain can always be aggregated to a coarser level to merge different sources of information or compare different forests. Furthermore, the hierarchy presented should not prevent any user from adopting an even finer grain with more levels (see below)

Form	Group	TreM type
Cavities l.s.	Woodpecker breeding cavities	Small woodpecker breeding cavity
		Medium-sized woodpecker breeding cavity
		Large woodpecker breeding cavity
		Woodpecker “flute” (breeding cavity string)
	Rot holes	Trunk base rot hole
		Trunk rot hole
		Semi-open trunk rot hole
		Chimney trunk base rot hole
		Chimney trunk rot hole
		Hollow branch
	Insect galleries	Insect galleries and bore holes
	Concavities	Dendrotelm (phytotelmata, water-filled hole)
		Woodpecker foraging excavation
		Trunk bark-lined concavity
		Root buttress concavity
Tree injuries and exposed wood	Exposed sapwood only	Bark loss
		Fire scar
		Bark shelter
		Bark pocket
	Exposed sapwood and heartwood	Stem breakage
		Limb breakage (heartwood exposed)
		Crack
		Lightning scar
		Fork split at the intersection
Crown deadwood	Crown deadwood	Dead branches
		Dead top
		Remaining broken limb
Excrescences	Twig tangles	Witch broom
		Epicormic shoots
	Burrs and cankers	Burr
		Canker
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting bodies	Perennial polypore
	Ephemeral fungal fruiting bodies and slime moulds	Annual polypore
		Pulpy agaric
		Large pyrenomycete
		Myxomycetes
Epiphytic and epixylic structures	Epiphytic and parasitic crypto- and phanerogams	Bryophytes
		Foliose and fruticose lichens
		Ivy and lianas
		Ferns
		Mistletoe
	Nests	Vertebrate nest
		Invertebrate nest
	Microsoils	Bark microsoil
		Crown microsoil
Exudates	Exudates	Sap run
		Heavy resinosis
7 forms	**15 groups**	**47 types**

Tableau 5 : Hierarchical typology of Tree-related Microhabitats in European temperate and Mediterranean forests. See Tableau 6 for type definitions and thresholds, and Tableau 7 Tableau 7for illustrations.

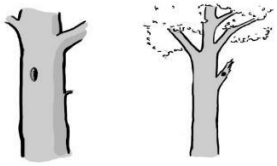
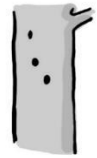
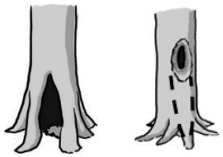
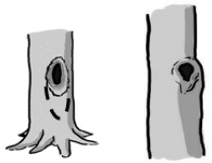
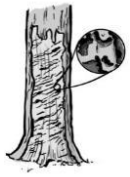
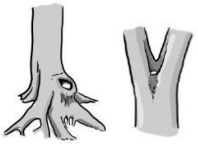
Tableau 6 : Tree related Microhabitat type definitions and inventory thresholds (Ø: diameter) for European temperate and Mediterranean forests.

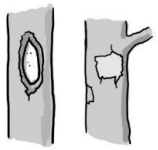
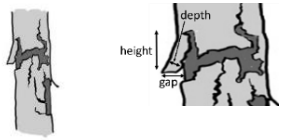
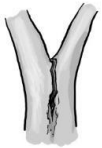
Type	Definition	Size threshold for inclusion in surveys	Threshold choice
Small woodpecker breeding cavity	Cavity entrance ø <4 cm. The breeding cavity of *Dendrocopos minor* is usually drilled in a dead branch.	Cavity entrance ø <4 cm	Biological, woodpecker size
Medium-sized woodpecker breeding cavity	Round cavity entrance about ø = 4-7 cm. The breeding cavities of the medium-sized woodpeckers (*Dendrocopos major*, *D. medius*, *D. leucotos*, *D. syriacus*, *Picus viridis*, *P. canus*, *Picoides tridactylus)* are usually drilled into decaying wood (dead branch, snag, insertion of broken-off branches).	Cavity entrance ø = 4-7 cm	Biological, woodpecker size
Large woodpecker breeding cavity	Oval cavity entrance ø >10 cm. The breeding cavities of *Dryocopus martius* are usually drilled on the main part of the trunk (without branches).	Cavity entrance ø > 10 cm	Biological, woodpecker size
Woodpecker "flute" (breeding cavity string)	At least three woodpecker breeding cavities in line on the trunk. Maximum distance of 2m between two consecutive cavities.	Cavity entrance ø > 3 cm	Biological, woodpecker size
Trunk base rot-hole	Cavity chamber is completely protected from surrounding microclimate and rain Top-closed trunk cavity containing more or less mould (depending on its development stage). The cavity bottom has ground contact. Note that the cavity entrance can be higher on the trunk.	Opening ø >10 cm	Biological, mammal size
Trunk rot-hole	Top-closed trunk cavity containing more or less mould (depending on its development stage). The cavity bottom has no ground contact.	Opening ø >10 cm	Biological, mammal size
Semi-open trunk rot-hole	Cavity chamber is not completely protected from surrounding microclimate and rain may flow in. Note that the cavity entrance can be higher up in the trunk	Opening ø >30 cm	Pragmatic
Chimney trunk base rot-hole	Cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage; the cavity base reaches ground level, so the inner cavity is in direct contact with the soil.	Opening ø >30 cm	Pragmatic
Chimney trunk rot-hole	Cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage; the cavity base does not reach ground level, so the inner cavity is not in direct contact with the soil.	Opening ø >30 cm	Pragmatic
Hollow branch	Rot hole in a large brach, resulting in a tubular shelter, often horizontally oriented.	Opening ø >10 cm	Pragmatic
Insect galleries and bore holes	A bore hole network of xylophagous insects indicates a wood hole system. An insect gallery is a complex system of holes and chambers created by one or more insect species in the wood.	Hole ø >2 cm or numerous smaller holes covering an area > 300 cm² (A5 format)	Pragmatic
Dendrotelm (phytotelmata, water-filled hole)	Cup-shaped concavity that, due to its form, retains water until it dries out by evaporation.	ø >15 cm	Biological, assemblage type
Woodpecker foraging excavation	Concavity resulting from the foraging activities of woodpeckers. The excavation is conical: the entrance is larger than the interior.	Depth> 10cm, ø >10cm	Biological, bird size
Trunk bark-lined concavity	Natural bark-lined concavity on the tree trunk. No mould.	Depth> 10cm, ø >10cm	Biological, bird size
Root buttress concavity	Natural bark-lined concavity at the base of the tree trunk formed by the tree roots and the soil. No mould (if so: see Trunk base rot hole)	Entrance ø >10 cm	Pragmatic
Bark loss	Loss of bark exposing sapwood (skinning caused *e.g.* by felling, skidding, natural tree fall, rock fall, rodents).	Area > 300 cm² (A5 format)	Pragmatic
Fire scar	Fire scars on the lower trunk. They usually have a triangular shape and are located at the base of the tree on the leeward side. Fire scars are associated with charcoal and sometimes resin flow on exposed sapwood or bark.	Area > 600 cm² (A4 format)	Pragmatic

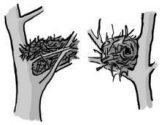
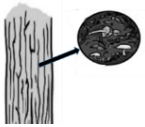
Type	Definition	Size threshold for inclusion in surveys	Threshold choice
Bark shelter	Space between peeled-off bark and sapwood forming a shelter (open at the bottom).	Gap > 1 cm; depth > 10 cm; height > 10 cm	Biological, Bat size
Bark pocket	Space between peeled-off bark and sapwood forming a pocket (open at the top) possibly containing mould.	Gap > 1 cm; width > 10 cm; height > 10 cm	Pragmatic
Stem breakage	The stem has broken off but the tree is still alive. The lower part of the deadwood is in contact with living wood with sap flow.	Stem ø > 20 cm at the broken point	Pragmatic
Limb breakage (heartwood exposed)	Exposed heartwood through limb or fork breakage. The wound is surrounded by living wood with sap flow.	Area of exposed heartwood > 300 cm² (A5 format)	Pragmatic
Crack	Crack through the bark and the wood (if caused by lightning strike, see below).	Length > 30 cm; width > 1 cm; depth > 10 cm	Biological, Bat size
Lightning scar	Crack caused by lightning strike; usually spiraling around the tree with splintered wood present.	Length > 30 cm; width > 1 cm; depth > 10 cm	Biological, Bat size
Fork split at the insertion	Crack at the insertion of a fork. (If one side of the fork has broken off, see Stem breakage).	Length >30cm	Pragmatic
Dead branches	Dead branches located in the canopy, conditions remain relatively shady.	Branch ø >10cm, or Branch ø >3cm and >10% of thecrown is dead	Pragmatic
Dead top	The entire top of the tree is dead; the deadwood is sun-exposed	ø >10cm at the lower part of the piece of deadwood	Pragmatic
Remaining broken limb	A limb has broken off. The remaining end may be splintered. The injury does not affect the trunk (If so, see Stem breakage).	Limb ø >20cm at the broken end; length of the remaining piece >0,5m	Pragmatic
Witch broom	Dense agglomeration of twigs on branches.	Largest ø >50cm	Pragmatic
Epicormic shoots	Dense agglomeration of twigs along the trunk.	>5 twig clusters	Pragmatic
Burr	Proliferation of cell growth with rough bark	Largest ø >20cm	Pragmatic
Decayed canker	Decayed canker. Sapwood exposed. Caused by *e.g. Melampsorella caryophyllacerum*, *Nectria* l. s.	Largest ø >20cm or large part of the trunk covered	Pragmatic
Perennial polypore	Tough fruiting bodies of perennial polypores, showing distinct annual tube layers. Main perennial genera: *Fomitopsis* pp, *Fomes*, *Perreniporia* pp., *Oxyporus*, *Ganoderma* pp, *Phellinus*, *Daedalea*, *Haploporus*, *Heterobasidion*, *Hexagonia*, *Laricifomes*, *Daedleopsis*.	Largest ø >5cm	Pragmatic
Annual polypore	Fruiting bodies of annual polypores, lasting several weeks. The European annual polypores have only one layer of tubes and are usually elastic and soft (no woody parts). Main annual genera: *Abortiporus, Amylocystis, Bjerkandera, Bondarzewia, Cerrena, Climacocystis, Fistulina, Gloeophyllum, Grifola, Hapalopilus, Inonotus, Ischnoderma, Laetiporus, Leptoporus, Meripilus, Oligoporus, Oxyporus, Perenniporia pp, Phaeolus, Piptoporus, Podofomes, Polyporus, Pycnoporus, Spongipellis, Stereum, Trametes, Trichaptum, Tyromyces*.	Largest ø >5cm or cluster of > 10 fruiting bodies	Pragmatic
Pulpy agaric	Large, thick and pulpy or rather fleshy fruiting body of gill-bearing fungi (order Agaricales). E.g. : *Armillaria, Pleurotus, Pholiota*, or large *Pluteus* species. The fruiting body generally remains several weeks.	Largest ø >5cm or cluster of > 10 fruiting bodies	Pragmatic
Large pyrenomycete	Large tough hemispheric dark fungi ressembling a lump of coal. e.g: *Daldinia* or *Hypoxylon*.	Stroma ø >3cm or stroma cluster covering >100cm²	Pragmatic

Type	Definition	Size threshold for inclusion in surveys	Threshold choice
Myxomycetes	Amoeboid slime mold which forms moving plasmodium. The plasmodium is gelatinous when fresh.	Largest ø >5cm	Pragmatic
Bryophytes	Trunk covered by mosses and liverworts.	>10% of the trunk area covered	Pragmatic
Foliose and fruticose lichens	Trunk covered by foliose or fruticose lichens.	>10% of the trunk area covered	Pragmatic
Ivy and lianas	Lianas and other climbing phanerogams (*Hedera helix, Clematis vitalba, Lonicera periclimenum, Vitis vinifera).*	>10% of the trunk area covered	Pragmatic
Ferns	Ferns growing directly on a part of a tree (*i.e.* epiphyte)	> 5 fronds	Pragmatic
Mistletoe	Epiphytic and hemiparasitic plants (*Viscum* spp., *Arceuthobium oxycedri, Loranthus europaeus*).	Largest ø >20cm	Pragmatic
Vertebrate nest	Nest built by birds, dormice, mice or squirrels.	ø >10cm	Biological, animal size
Invertebrate nest	Larval nest of invertebrates: *e.g.* Pine processionary moth *Thaumetopoea pityocampa*, wood ant *Lasius fuliginosu*s or wild bees *Apis mellifera*.	Presence	Pragmatic
Bark microsoil	Microsoil resulting from micro-pedogenesis of epiphytic mosses, lichens or algae and necrosed old, thick bark.	Presence	Pragmatic
Crown microsoil	Microsoil resulting from pedogenesis of debris and litter fall from the crowns, often colonized by roots of the TreM bearing-tree. Main positions: flat areas, forks, stem junctions of twin trees.	Presence	Pragmatic
Sap run	Fresh significant flow of sap.	Cumulative length >10 cm	Pragmatic
Heavy resinosis	Fresh significant flow of resin.	Cumulative length >10 cm	Pragmatic

Tableau 7 : Illustrations of the TreM types in European temperate and Mediterranean forest.

Form	Group	Types					
Cavities l.s.	Woodpecker breeding cavities	**Small woodpecker breeding cavity** Entrance ø<4cm 	**Medium-sized woodpecker breeding cavity** Entrance ø = 4-7cm 	**Large woodpecker breeeding cavity** Entrance ø >10cm 	**Woodpecker flute** Entrance ø > 3cm 		
	Rot-holes	**Trunk base rot-hole (closed top, ground contact)** Opening ø >10cm 	**Trunk rot-hole (closed top, no ground contact)** Opening ø >10cm 	**Semi-open trunk rot-hole** Opening ø >30cm 	**Chimney trunk base rot-hole** Opening ø >30cm 	**Chimney trunk rot-hole** Opening ø >30cm 	**Hollow branch** Opening ø >10cm 
	Insect galleries	**Insect galleries and bore holes** Hole ø >2cm or area >300cm² 					
	Concavities	**Dendrotelm** ø >15cm 	**Woodpecker foraging excavation** Depth >10cm, ø >10cm 	**Trunk bark-lined concavity** Depth >10cm, ø >10cm 	**Root-buttress concavity** Entrance ø >10cm 		

Form	Group	Types					
Tree injuries and exposed wood	Exposed sapwood only	**Bark loss** Area > 300cm² 	**Fire scar** Area > 600cm² 	**Bark shelter** Gap >1cm, depth >10cm, height>10cm 	**Bark pocket** Gap >1cm, width >10cm, height>10cm 		
	Exposed sapwood and heartwood	**Stem breakage** ø >10cm at break point 	**Limb breakage** Exposed heartwood >300cm² 	**Crack** Length > 30 cm, width > 1 cm, depth > 10 cm 	**Lightning scar** Length > 30 cm, width > 1 cm, depth > 10 cm 	**Fork split at insertion** Length > 30 cm 	
Crown deadwood	Crown deadwood	**Dead branches** Branch ø >10cm, or Branches ø >3cm and >10% of the crown is dead 	**Dead top** ø >10cm at the base of the piece of deadwood 	**Remaining broken limb** broken end ø >20cm, length of the remaining piece >0.5m 			
Excrescences	Twig tangles	**Witch broom** Largest ø >50cm 	**Epicormic shoots** >5 twig clusters 				
	Burrs and cankers	**Burr** Largest ø >20cm 	**Canker** Largest ø >20cm or large part of the trunk covered 				

Form	Group	Types					
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting	**Perennial polypore** Largest ø >5cm 					
	Ephemeral fungal fruiting bodies	**Annual polypore** Largest ø >5cm or cluster of > 10 fruiting bodies 	**Pulpy agaric** Largest ø >5cm or cluster of > 10 fruiting bodies 	**Large pyrenomycete** Stroma ø >3cm or stroma cluster covering >100cm² 	**Myxomycetes** Largest ø >5cm 		
Epiphytic and epixylic structures	Epiphytic and parasitic crypto- and phanerogams	**Bryophytes** >10% of the trunk area covered 	**Foliose and fruticose lichens** >10% of the trunk area covered 	**Ivy and lianas** >10% of the trunk area covered 	**Ferns** > 5 fronds 	**Mistletoe** Largest ø >20cm 	
	Nests	**Vertebrate nest** ø >10cm 	**Invertebrate nest** Presence 				
	Microsoils	**Bark microsoil** Presence 	**Crown microsoil** Presence 				
Exudates	Exudates	**Sap run** Cumulative length >10 cm 	**Heavy resinosis** Cumulative length >10 cm 				

3.2. Protocol guidelines for standardized TreM surveys

In order to produce standardized and comparable TreM surveys, a certain number of standardized inventory protocols must be applied to the unequivocal definitions and threshold sizes of the TreM types detailed above.

A wide range of survey approaches can be applied, depending on specific objectives, requirements or circumstances. However, some basic rules should be respected in order to perform quality TreM surveys with limited observer effects (Paillet et al., 2015a) and high reliability (accuracy, repeatability and practical performance). We have assumed that classical forest protocols already include basic tree data such as diameter at breast height (dbh), tree species and status (dead or alive). TreM records will therefore complement this classical survey data. Based on this assumption, we propose a set of requirements that are to be met, in order to allow *a posteriori* compilation and comparison of datasets including TreM inventories. For the most detailed and intensive survey level (*e.g.* scientific studies), we also specify additional features that could complement TreM inventories for a finer description and characterisation of specific TreM types (Annexe 2).

3.2.1. TreM inventories: survey baseline

The three levels of the hierarchical typology reflect three specific survey objectives: (i) the first level (*i.e.* Forms) could be used for quickscans of TreM-bearing trees during forest management operations (*e.g.* tree selection and marking); (ii) the second level of hierarchy (*i.e.* Groups) could be applied in routine surveys and inventories (NFI, management plan and Natura 2000 inventories); (iii) the third, most detailed, level (*i.e.* Types) could be applied in scientific surveys, with the possibility, depending on the objective of the study, to further subdivide and characterise the individual TreMs (according to the elements indicated in Annexe 2, see below).

Ideally, TreM inventories should be made by a team of two observers, especially for routine inventories and scientific surveys. Even though a single trained observer may be able to perform a good survey, double observation is assumed to be more complete and systematic and to reduce observer effects (Paillet et al., 2015a). Every eligible tree is visually checked for TreMs from all directions from the root base up to the crown. One thorough inspection from all sides may be sufficient, but we suggest a minimum of two turns around a tree (*e.g.* one for the trunk base and lower trunk up to eye-level, and another one to inspect the upper trunk and tree crown); this may sometimes be difficult and time-consuming when the field conditions are rough (*e.g.* steep slope). Individual tree surveys may take from one to three minutes, depending on the slope, tree dimensions and level of detail required (*i.e.* the typology grain selected). This time per tree is only an estimation based on field experience and should be confirmed by field trials applied to a specific objective (*e.g.* surveys by NFI teams).

During routine inventories, no specific field equipment is required other than binoculars, which are essential for checking TreMs high on the trunk or in the tree crown, especially smaller features such as branch cavities or breeding cavities of medium-sized woodpeckers. For more intensive surveys like detailed cavity studies, other tools such as pole cameras or drones (Steich et al., 2016) may be helpful in assessing the characteristics of cavities (inner volume, presence/absence of mould). In broadleaved-dominated stands, it is highly advisable to record TreMs only after leaf fall because some small TreMs high in the canopy (dead branches, epiphytes) are difficult to see through the tree's leaves; a high, thick understory often limits visibility as well.

The present recommendations do not impose any dbh or height threshold for TreM inventories. The 'relevant' dbh will depend on the specific objectives and local circumstances, but it should be borne in mind that the higher the dbh, the fewer the trees checked, and the lower the workload. For comparative studies, the dataset with the highest dbh or height threshold value will logically determine the subset of data that can be used for comparison. Furthermore, even if the proportion of TreM-bearing trees increases dramatically with increasing dbh class (Larrieu and Cabanettes, 2012; Michel et al., 2011; Paillet et al., 2017; Winter et al., 2015b), medium-sized trees may account for a significant proportion of certain types (Larrieu et al., 2012; Paillet et al., 2017). Therefore, minimum dbh-limit

should not be above 30 cm; we recommend lower values (*e.g.* 10 cm dbh), particularly for research surveys.
Observed TreMs may be listed per tree (occurrence) or counted (abundance on each tree) in a quantitative (*e.g.* number of conks or woodpecker cavities, etc.) or semi-quantitative way (*e.g.* percentage classes of exposed heartwood). Most TreMs can be recorded for both living trees and snags (Tableau 6). However, some TreM types occur on living trees only (*e.g.* sap runs, mistletoe).

3.2.2. Optional TreM features for intensive surveys

Observing TreM attributes in detail will provide a better understanding of TreM dynamics, both at the TreM scale (*i.e.* evolving or decay processes) and at the stand scale (*i.e.* TreM profile dynamics). We present in Annexe 2 an extensive set of recordable attributes for each TreM. The set covers additional size specifications (inner and outer dimensions), decay stage, position on the tree, content (*e.g.* amount of mould in rot holes) and other TreM characteristics (*e.g.* simple vs splintered for trunk breakage). These attributes may be recorded during intensive monitoring or research operations since they may be of particular importance for specific taxa. They may also be considered as TreM sub-types, though we did not include them as such in this typology in the interest of simplicity. For each quantifiable feature, we propose recording either the absolute dimension (size, height, surface area) or using a semi-quantitative scale (*e.g.* cover classes, 10-25% of the total trunk area…). For some TreM types, we also suggest setting additional thresholds or further spliting down size classes to record smaller-sized features. Three drawing referentiels are also proposed to quickly identify evolving stages of rot holes and bark loss, and life stages of perennial polypores (Annexe 2).

4. Discussion

4.1. To include or not to include: TreM definition and typology relevance

Establishing standards and typologies is a prerequisite for any type of monitoring. The typology we present in this paper with its 47 TreM types should help standardize TreM inventories and make comparative studies possible. To build this typology, we used mainly morphological characteristics to categorize the TreMs since morphology is the simplest criterion to differentiate such structures in the field. Second, we categorized TreM groups by the substrates they supply. To determine the eligibility of a given TreM to the typology and its hierarchical position, we primarily considered its taxa relevance and its pertinence in terms of their life-history traits (*e.g.* the Frisbee database, Bouget et al., 2008, for saproxylic beetles; or Syrph the Net, Speight et al., 2013, for hoverflies). We carried out exploratory clustering analyses based on the substrates supplied (Larrieu, 2014) and on complementary expert knowledge.

Such a typology may appear too simplistic as a surrogate for direct biodiversity assessment since several species groups such as arthropods select their habitats according to their chemical markers (for example, emanations from the decaying process; see *e.g.* Gouix, 2011), rather than their physical features (*e.g.* Schmidl et al., 2008). To cope with this limitation, supplementary attributes (*e.g.* epiphyte hiding the entrance of a woodpecker breeding cavity) or characteristics (*e.g.* sun-exposed vs shaded dead branches) could be inventoried in intensive studies to differentiate species assemblages that coexist within the same TreM type. This may help to specify the functional links between biodiversity and TreM substrates. However, many TreM types could also be viewed as a composite of several subtypes that are impossible to delineate individually in the field, despite their importance for certain highly specialized taxa (such as the different beetle assemblages living in the three parts of a conk of saproxylic fungi: the trama, the pores or the interface between the conk and the bark, see *e.g.* Nikitsky and Schigel, 2004).

Inversely, the typology may appear too detailed for some practitioners. Here, its hierarchical structure provides adaptability to various contexts and objectives. In particular, information from different

studies or inventories can always be aggregated to a coarser grain in the topology in a coherent and compatible way in order to compile and compare different datasets (see *e.g.* Larrieu et al., 2014b).

4.2. Relevance of thresholds and guidelines

In theory, to fully assess the role TreMs play in biodiversity, all the TreMs on a given tree should be recorded, whatever their size or position, since they all provide resources for associated communities. This means, however, so that there would be an infinite number of TreMs for a given tree. In practice, comprehensive recording of TreMs is virtually impossible and, even with simplified lists, observer effects are strong (Paillet et al., 2015a). It is therefore crucial to define thresholds in order to reduce (i) the time devoted to the survey, and (ii) the observer-related biases. Definiting thresholds increases replicability and thereby improves the quality of the data. Most of the thresholds we have defined here are based on recording practicality ("pragmatic" thresholds, *e.g.* a minimum area of a missing bark for observing it easily whatever its position on the trunk), though thresholds for 13 TreM types are based on biological evidence and features (such as the mean diameter of a breeding cavity for a woodpecker species). A few focus on a target taxon (*e.g.* thresholds for crack width correspond to bat species requirements). We feel that both threshold parameters and a description of features are essential to standardize the records. Including these two types of data makes a clear and unequivocal delineation for TreM records possible and allows comparisons to be made among different studies throughout European forests. These proposed thresholds may be modified in the future if other values are found to be more ecologically relevant (*i.e.* based on scientific evidence) but, in case of changes, sensitivity analyses should be performed to be sure that detectability levels in the field remain acceptable. In other words, the typology presented in this paper may be adapted as scientific knowledge develops, but with respect to the proposed hierarchical approach.

It may not always be possible to restrict TreMs surveys to periods after leaf fall, for example, in particular contexts (*e.g.* in mountain forests where inventories are preferably performed in summer), stand types (*e.g.* those dominated by evergreen broadleafs or conifers) or wide-scale inventories (a significant proportion of National Forest Inventories are performed during the vegetation period). TreM records during the vegetation period require more time to reliably check the tree and may make recording certain TreM types very difficult (*e.g.* crown cavities). Inversely, some types, such as crown deadwood on living trees, may be easier to identify during the vegetation period. In any case, as inventories are performed at different periods of the year, the date of inventory should be included in subsequent analyses to correct for possible variations due to potential observation biases.

The part of the tree that is to be observed during TreM surveys can also be modified. Branches (and leaves on conifers and evergreen species) can hide parts of the trunk; therefore recording TreMs on the first meters of the trunk only would be less time–consuming and would help minimize observer effect. Moreover, close range observation does not require binoculars and reduces the risk of misinterpretation (*e.g.* dendrotelms). However, few TreM types are exclusively found on the lower part of the trunk (*e.g.* root-buttress concavities) and certain TreM types are specific to the crown (*e.g.* witch brooms). Furthermore, cavities suitable for bats are mainly borne by large healthy branches (*e.g.* Tillon and Aulagnier, 2014), and crown deadwood hosts very specific beetle assemblages (Bouget et al., 2011). We recommend observing at least the whole trunk from the ground to the crown base and its main sub-vertical limbs, and to complete the inventory by recording crown deadwood.

4.3. Limitations of the typology

The typology presented herein is mainly valid for European temperate and Mediterranean forests; indeed, the scientists co-authoring this paper are experts in this field. As a consequence, TreMs specific to other forest types might be under-represented. For example, in this typology, only one TreM type (fire scars) has a charred wood substrate, while TreMs linked to wildfire certainly provide valuable

substrates for a large number of species in the boreal biome, where wildfires are typical (*e.g.* Gibb et al., 2006; Hjältén et al., 2012). This is probably also true for the Mediterranean biome, though to a lesser extent (Bouget et al., 2008). Similarly, since woodpeckers do not occur in Australasia (Cockle et al., 2011), the TreM group *woodpecker breeding cavities* is not relevant for e.g. , Australian temperate forests. However, our typology is flexible enough to be complemented and further adapted for use in forest types outside our initial predefined area of application, at least in boreal or non-European temperate forests.

We also designed this typology mainly for living trees and standing deadwood. However, certain TreMs may also occur on lying deadwood. For example, conks of fungi, Myxomycetes, dendrotelms or woodpecker feeding holes regularly occur on lying pieces of deadwood (Bobiec et al., 2005), and contribute to the total supply at the stand scale. Furthermore, lying deadwood contains microhabitats that are not covered in this typology (*e.g.* specific mould and microsoil conditions of highly decayed wood, pit and mound structures and microtopographies). Therefore, recording TreMs on standing trees only (living and dead) may lead to an underestimation of what should be taken into account in studies which focus on the relationship between TreMs and biodiversity at the stand scale. In this case, sampling should include TreMs on lying deadwood and the typology should be adapted accordingly.

4.4. Perspectives for research

4.4.1. TreMs and environmental characteristics

At the tree scale, the link between TreM richness or diversity and tree characteristics, *e.g.* trunk diameter or tree vitality, has already been studied (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011; Winter et al., 2015b; Winter and Möller, 2008). However, these studies concern only a limited number of tree species (mainly *Fagus sylvatica* L. and *Abies alba* Mill.). In addition, the links between TreMs and tree characteristics are likely to vary with site and climatic conditions such as soil type and fertility, elevation and humidity; other abiotic factors such as rockfalls, avalanches and snow or thunderstorms can also generate TreMs. The effects of these environmental factors on TreM development have rarely been studied due to the limited number of large datasets (either in number of observations or spatial extent) and to the difficulty of clearly identifying the origin of certain TreMs. A few studies have tested co-occurrences and correlations among TreMs (*e.g.* Larrieu and Cabanettes, 2012; Regnery et al., 2013b; Winter et al., 2015b) but, in order to better understand how TreMs appear and change over time, these studies should be complemented by further comparable tests, based, whenever possible, on data from long-term surveys on permanent plots. Ultimately, this would make it possible to simplify the typology based on co-occurrence patterns.

At the stand scale, Bouget et al. (2014), Larrieu et al. (2012), Larrieu et al. (2016), Michel and Winter (2009), Paillet et al. (2017), and Winter et al. (2005) have investigated how TreM profiles are affected by setting aside forest reserves and by time since management abandonment. Indeed, there is a general trend towards higher densities of TreMs in strict reserves and when forests have been left unmanaged for a long time. But studying only TreM densities rather than the TreM profile may mask compensations between TreM types typical for managed or unmanaged sites; and the response may vary with the indices used (*i.e.* abundance vs occurrence data). For example, Paillet et al. (2017) showed that the overall density of TreMs at the stand level was higher in strict forest reserves than in their managed counterparts and that the magnitude of this difference varied with elevation. Conversely, Larrieu et al. (2012) showed that the number of TreMs was not always higher in unmanaged stands since dendrotelms and missing bark were favoured by logging; however, they did find that TreM diversity was lower in managed stands than in near-natural forests. To confirm these findings, reference studies in the rare primeval temperate forests, in Europe or elsewhere, are much needed (see *e.g.* Commarmot et al., 2013). Studying remnants of primeval forests could also help us understand the spatial distribution of TreMs under natural conditions. More generally, the effects of different management types (silvicultural regimes) on TreMs have rarely been tested (Michel and

Winter, 2009). Finally, microhabitat dynamics have not been studied over time. Long-term monitoring or modeling is necessary to better understand the genesis and mechanisms that drive microhabitat dynamics (see Siitonen, 2012).

4.4.2. TreMs and biodiversity

Some TreM types (*e.g.* mould cavities) harbour high species richness and host many different taxonomic groups, while some TreM types (*e.g.* dendrotelms) harbour few species belonging to only a few taxonomic groups. Nevertheless, conservation value cannot only be defined by the number of species using a given TreM type; we should also consider the occurrence of species exclusively conditioned to a single TreM type. That is why we combined scientific information and expert knowledge to build a typology based on TreM substrate availability and biodiversity relevance.

At the stand scale, most of the references related to the ecological role of TreMs are limited to certain forest ecosystems and taxonomic groups, mainly saproxylic beetles (*e.g.* Bouget et al., 2014; Bouget et al., 2013; Lassauce et al., 2013; Winter and Möller, 2008) and hoverflies (*e.g.* Herrault et al., 2016; Larrieu et al., 2015) in temperate forests, and birds and bats (*e.g.* Regnery et al., 2013a) in Mediteranean forests. Evidently, the link between some species groups and TreM types remains unknown or requires stronger scientific evidence. Specific research (*i.e.* correlative analyses at tree and stand scales) is still needed to confirm the role of certain TreMs as a substrate for biodiversity in European forest ecosystems. In particular, analyzing TreM characteristics as specified in Annexe 2 may help us better understand the ecological mechanisms involved in the relation between TreM substrates and biodiversity.

At the landscape scale, very few studies have assessed the effects of TreM densities on biodiversity, with the following exceptions: cavities and birds (*e.g.* Robles and Martin, 2014), hollow trees and beetles (*e.g.* Ranius et al., 2010), and a set of TreM types and hoverflies (Herrault et al., 2016). In particular, it is unclear wether a single tree bearing a combination of TreM types is equivalent to several trees bearing the same combination of single TreM types. This question, also referred to as the SLOSS – Single Large Or Several Small – debate (Ovaskainen, 2002; Tjørve, 2010), has, to our knowledge, not been assessed in European forests (but see Le Roux et al., 2015 for an example in Australia). More information is therefore needed to determine the density and spatial distribution of TreMs required to conserve their associated biodiversity or to enhance populations of rare or endangered specialized species.

5. Conclusions: Tree related Microhabitats as a monitoring and management tool

For forest managers, TreMs have long been seen as damage or defects to trees which negatively affect timber production. Especially where high quality timber was the main production goal, trees with high TreM potential such as forked, leaning or bizarrely shaped trees (Bütler et al., 2013) and so called “wolf trees” (with undesired overgrowth) were subject to negative selection when competing with trees of promising quality. Additionally, old senescent trees as well as snags are often considered hazardous to workers and the public and are systematically removed. Thus, TreM-bearing habitat trees are currently rare in managed forests in Europe (Bütler and Lachat, 2009; Larrieu et al., 2014a; Larrieu et al., 2012; Larrieu et al., 2014b; Paillet et al., 2017; Winter and Möller, 2008). Furthermore, the situation is likely to deteriorate if positive selection strategies are not applied more widely to secure a continuous supply of trees with TreM potential along with the production of merchantable trees. Nowadays, however, the retention of habitat trees (including TreMs-bearing trees) is increasingly being recognized as necessary, both in forest management (Kraus and Krumm, 2013) and policy (Ministerium für Landwirtschaft Umweltschutz und Raumordnung, 2004; Winter et al., 2015a). TreMs’ ecological value is increasingly being emphasized, and efforts are being made to integrate their conservation into modern multi-functional forestry (Bütler et al., 2013; Flade et al., 2004; Larrieu et al., 2014a; Michel

and Winter, 2009; Winter et al., 2015a). In particular, the Natura 2000 European network promotes the conservation of habitat trees as a tool to ensure the long term survival of threatened species, but the characterizations of habitat trees and microhabitats remains rather vague and heterogeneous (European Commission, 2015).

Our proposed TreM definition and typology, along with our guidelines for standardized survey protocols, represent a first step towards a standardized method for inventorying TreMs and conserving of habitat trees. This work will ensure reproducibility and high data quality, and aims to provide a basic guarantee that the methods used to gather data by various operators are standardized (Allegrini et al., 2009; Ferretti, 2009, 2013; Paillet et al., 2015a). In particular, we expect that implementing the typology at various scales and for various purposes will make data comparable across national inventories, and help establish references at a large international scale. The list is open and adapted to further developments based on increasing scientific knowledge, as suggested above. However, we believe the typology in its current form is already valid, particularly for scientific studies and monitoring purposes, and can henceforth be used to evaluate the success of policies designed to achieve (larger-scale) nature conservation. Indeed, Kraus et al. (2016)'s European TreM field guide initiative is largely based on the present work and has already been translated into several languages and applied in a wide range of ecological conditions (see also the tablet and smartphone applications used to vulgarize TreMs, available at http://www.integrateplus.org/m-learning-tools.html).

The present study clearly shows that TreMs support a wide array of biodiversity that is not usually supported by other forest structures. From a monitoring point of view, information about TreMs is complementary to data on features traditionally classified under forest structure (dimensions, tree species) and deadwood (type, dimension, decay stage). Understanding the factors that influence the occurrence and distribution of TreMs, their link with biodiversity and quantifying the potential observer effect would ultimately help validate TreMs as biodiversity indicators (Paillet et al., 2015a). In particular, comparing the performance of TreMs with that of other indicators (*e.g.* those used for reporting on the State of Europe's Forests) is much needed (Gao et al., 2015). We expect TreMs to play a complementary (or combined) role with other existing biodiversity indicators such as deadwood profile or tree species diversity. Integrating TreM preservation into common forest management practices may help slow forest biodiversity loss while TreM monitoring may prove to be an additional tool for assessing the state of biodiversity in European forests.

Acknowledgements and funding

We are grateful to the Integrate+ project ("Establishing a European network of demonstration sites for the integration of biodiversity conservation into forest management") for financial and technical support (TreM illustrations). Integrate+ was funded by the German Federal Ministry for Food and Agriculture (BMEL) and was coordinated by the European Forest Institute (EFI).

We are grateful to the Research and Development project „Umsetzung von Zielen der Nationalen Biodiversitätsstrategie in Wäldern: Untersuchung des Einflusses von naturschutzorientierter Bewirtschaftung auf Naturnähe und Biodiversität von Tiefland-Buchenwäldern", FKZ 3511 84 0100, for financial support. The above project was funded by the Federal Agency of Nature Conservation, Bonn, Germany.

Many thanks to Mathias Vust, Switzerland, who provided information on the habitat requirements of lichens, to Lisa Apfelbacher (Germany) for the illustrations of the TreMs, to Christophe Bouget, Marc Deconchat, Peter Meyer, Fabio Lombardi and Michael Rzanny who significantly contributed to the emergence of this hierarchical typology, and to Tim Green (EFI) and Vicki Moore for their thorough editing of the English style and for general work on the manuscript. Thanks also to Gilles Corriol, Maria Infante-Sanchez, Christophe Bouget and Luc Barbaro for checking Tableau 4.

References

Allegrini, M.C., Canullo, R., Campetella, G., 2009. ICP-Forests (International Co-operative programme on assessment and monitoring of Air pollution effects on forests): Quality assurance procedure in plant diversity monitoring. J. Environ. Monit. 11, 782-787.

Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P., Laudenslayer, W.F., 2005. The afterlife of the tree. WWW Poland, Warszawa-Hajnowka.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the " last biotic frontier": Are temperate forest canopies special for saproxylic beetles? For. Ecol. Manag. 261, 211-220.

Bouget, C., Brustel, H., Zagatti, P., 2008. The FRench Information system on Saproxylic BEetle Ecology (FRISBEE): An ecological and taxonomical database to help with the assessment of forest conservation status. Revue d'Ecologie (La Terre et la Vie) 63, 33-36.

Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecol. Indic. 36, 656-664.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers. Conserv. 22, 2111-2130.

Bütler, R., Lachat, T., 2009. Wälder ohne Bewirtschaftung: eine Chance für die saproxylische Biodiversität. Schweizerische Zeitschrift fur Forstwesen 160, 324-333.

Bütler, R., Lachat, T., Larrieu, L., Paillet, Y., 2013. Habitat trees: key elements for forest biodiversity, in: Kraus, D., Krumm, F. (Eds.), Integrative approaches as an opportunity fir the conservation of forest biodiversity. European Forest Institute, Freiburg, DEU, pp. 84-91.

Carvalho, F., Carvalho, R., Mira, A., Beja, P., 2014. Use of tree hollows by a Mediterranean forest carnivore. For. Ecol. Manag. 315, 54-62.

Chirici, G., McRoberts, R.E., Winter, S., Bertini, R., Bröändli, U.B., Asensio, I.A., Bastrup-Birk, A., Rondeux, J., Barsoum, N., Marchetti, M., 2012. National forest inventory contributions to forest biodiversity monitoring. For. Sci. 58, 257-268.

Christensen, M., Hahn, K., Mountford, E.P., Odor, P., Standovar, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. For. Ecol. Manag. 210, 267-282.

Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9, 377-382.

Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V., 2013. Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf; Ukrainian National Forestry University, L'viv; Carpathian Biosphere Reserve, Rakhiv.

Convention on Biological Diversity, 1992. Convention on Biological Diversity. Secretariat of the Convention on Biological Diversity (CBD). United Nations Environment Programme., p. 83.

Dajoz, R., 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier. Tec & Doc Lavoisier, Paris.

European Commission, 2015. Natura 2000 and forests. EU publications, Luxembourg.

European Environmental Agency, 2008. European forests - ecosystem conditions and sustainable use. European Environmental Agency (EEA), Copenhagen.

Ferretti, M., 2009. Quality Assurance in ecological monitoring - Towards a unifying perspective. J. Environ. Monit. 11, 726-729.

Ferretti, M., 2013. A quality assurance framework for designing forest monitoring programs, in: Ferretti, M., Fischer, A. (Eds.), Forest monitoring. Methods for terrestrial investigation in Europe with an overview of North America and Asia, 1st ed. Elsevier, pp. 77-90.

Finn, J.A., 2001. Ephemeral resource patches as model systems for diversity-function experiments. Oikos 92, 363-366.

Flade, M., Möller, G., Schumacher, H., Winter, S., 2004. Naturschutzstandards für die Bewirt-schaftung von Buchenwäldern im nordostdeutschen Tiefland. Der Dauerwald - Zeitschrift für naturgemäße Waldwirtschaft 29, 15-28.

Food and Agriculture Organization, 2015. Global Forest Resources Assessment 2015. Food and Agriculture Organizationof the United Nations,, Rome, p. 253.

Forest Europe, 2015. State of Europe's Forests 2015.

Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol. Indic. 57, 420-434.

Gibb, H., Hjältén, J., P. Ball, J., Atlegrim, O., Pettersson, R.B., Hilszczanski, J., Johansson, T., Danell, K., 2006. Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: A study using experimental logs for monitoring assemblages. Ecography 29, 191-204.

Gossner, M.M., Lade, P., Rohland, A., Sichardt, N., Kahl, T., Bauhus, J., Weisser, W.W., Petermann, J.S., 2016. Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry. J. Anim. Ecol. 85, 213-226.

Gouix, N., 2011. Gestion forestière et Biodiversité, les enjeux de conservation d'une espèce parapluie : Limoniscus violaceus (Coleoptera). Université Pierre et Marie Curie, Paris 6, p. 260.

Gouix, N., Brustel, H., 2012. Emergence trap, a new method to survey Limoniscus violaceus (Coleoptera: Elateridae) from hollow trees. Biodivers. Conserv. 21, 421-436.

Halama, M., Chachuła, P., Rutkowski, R., 2014. Mycena juniperina (Agaricales, Basidiomycota), new for the polish and central European Mycobiota. Pol. Bot. J. 59, 109-116.

Herrault, P.A., Larrieu, L., Cordier, S., Gimmi, U., Lachat, T., Ouin, A., Sarthou, J.P., Sheeren, D., 2016. Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae). Landsc. Ecol. 31, 877-893.

Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczański, J., 2012. Micro and macro-habitat associations in saproxylic beetles: Implications for biodiversity management. PLoS ONE 7.

Hunter, M.L.J., 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, p. 698.

Jahns, H.M., 1989. Guide des fougères, mousses et lichens d'Europe. Delachaux & Niestlé, Neuchâtel, Switzerland.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., Winter, S., 2016. Catalogue of tree microhabitats – Reference field list. Integrate+ Technical Paper, European Forest Insitute, Freiburg, Germany.

Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg, Germany.

Larrieu, L., 2014. Les dendro-microhabitats : facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique, Dynamiques et écologie des paysages agriforestiers - DYNAFOR UMR 1201. Institut National Polytechnique de Toulouse, Toulouse, France, p. 111 + Annexes.

Larrieu, L., 2016. Vers une typologie pratique et écologiquement pertinente des microhabitats des arbres, in: Vallauri, D., Chauvin, C., Brun, J.J., Fuhr, M., Sardat, N., André, J., Eynard-Machet, R., Rossi, M., De Palma, J.P. (Eds.), Naturalité des eaux et des forêts. Tec & Doc, Lavoisier, pp. 77-84.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can. J. For. Res. 42, 1433-1445.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014a. Tree microhabitats at the stand scale in montane beech-fir forests: Practical information for taxa conservation in forestry. European Journal of Forest Research 133, 355-367.

Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. European Journal of Forest Research 131, 773-786.

Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., Deconchat, M., 2014b. Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring. For. Ecol. Manag. 334, 163-173.

Larrieu, L., Cabanettes, A., Gouix, N., Burnel, L., Bouget, C., Deconchat, M., 2016. Development over time of the tree-related microhabitat profile: the case of lowland beech–oak coppice-with-standards set-aside stands in France. European Journal of Forest Research, 1-13.

Larrieu, L., Cabanettes, A., Sarthou, J.P., 2015. Hoverfly (Diptera: Syrphidae) richness and abundance vary with forest stand heterogeneity: Preliminary evidence from a montane beech fir forest. Eur. J. Entomol. 112, 755-769.

Larsson, T.B., 2001. Biodiversity evaluation tools for European forests. Ecol. Bull. 50, 1-237.

Lassauce, A., Larrieu, L., Paillet, Y., Lieutier, F., Bouget, C., 2013. The effects of forest age on saproxylic beetle biodiversity: Implications of shortened and extended rotation lengths in a French oak high forest. Insect Conservation and Diversity 6, 396-410.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D., Gibbons, P., 2015. Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. Biol. Conserv. 191, 558-566.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Franklin, J.F., 2000. Structural features of old-growth Australian montane ash forests. For. Ecol. Manag. 134, 189-204.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433-445.

Martin, K., Eadie, J.M., 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manag. 115, 243-257.

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. For. Ecol. Manag. 257, 1453-1464.

Michel, A.K., Winter, S., Linde, A., 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (Pseudotsuga menziesii var. menziesii). Can. J. For. Res. 41, 300-308.

Ministerium für Landwirtschaft Umweltschutz und Raumordnung, 2004. Waldbau-Richtlinie „Grüner Ordner“ der Landesforstverwaltung Brandenburg. Ministerium für Landwirtschaft, Umweltschutz und Raumordnung (MLUR) des Landes Brandenburg p. 143.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research, 981-992.

Nikitsky, N.B., Schigel, D.S., 2004. Beetles in polypores of the Moscow region: Checklist and ecological notes. Entomol. Fenn. 15, 6-22.

Ovaskainen, O., 2002. Long-term persistence of species and the SLOSS problem. J. Theor. Biol. 218, 419-433.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manag. 389, 176-186.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F., Gosselin, F., 2015a. Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. Ecol. Indic. 49, 14-23.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015b. Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. For. Ecol. Manag. 346, 51-64.

Ranius, T., 2002. Osmoderma eremita as an indicator of species richness of beetles in tree hollows. Biodivers. Conserv. 11, 931-941.

Ranius, T., Johansson, V., Fahrig, L., 2010. A comparison of patch connectivity measures using data on invertebrates in hollow oaks. Ecography 33, 971-978.

Ranius, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (Quercus robur). For. Ecol. Manag. 257, 303-310.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., Kerbiriou, C., 2013a. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Indic. 34, 221-230.

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013b. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? For. Ecol. Manag. 295, 118-125.

Remm, J., Lõhmus, A., 2011. Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manag. 262, 579-585.

Robles, H., Martin, K., 2014. Habitat-mediated variation in the importance of ecosystem engineers for secondary cavity nesters in a nest web. PLoS ONE 9.

Rondeux, J., Bertini, R., Bastrup-Birk, A., Corona, P., Latte, N., McRoberts, R.E., Ståhl, G., Winter, S., Chirici, G., 2012. Assessing deadwood using harmonized national forest inventory data. For. Sci. 58, 269-283.

Saunders, D.A., Mawson, P.R., Dawson, R., 2014. Use of tree hollows by Carnaby's Cockatoo and the fate of large hollow-bearing trees at Coomallo Creek, Western Australia 1969-2013. Biol. Conserv. 177, 185-193.

Schmidl, J., Sulzer, P., Kitching, R.L., 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: Community composition reflects structural, trophic and physicochemical factors. Hydrobiologia 598, 285-303.

Siitonen, J., 2012. Microhabitats, in: Stokland, J.N., Siitonen, J., Jonsson, B.G. (Eds.), Biodiversity in dead wood. Cambridge University Press, New York, USA, pp. 150-182.

Speight, M.C.D., Castella, E., Sarthou, J.P., 2013. StN 2013, in: Speight, M.C.D., Castella, E., Sarthou, J.-P., Vanappelghem, C. (Eds.), Syrph the Net on CD, Issue 9. The database of European Syrphidae. Syrph the Net Publications, Dublin.

Steich, K., Kamel, M., Beardsley, P., Obrist, M.K., Siegwart, R., Lachat, T., 2016. Tree cavity inspection using aerial robots, 2016 IEEE/RSJ International Conference on Intelligent Robots and Systems, IROS 2016. Institute of Electrical and Electronics Engineers Inc., pp. 4856-4862.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. University Press, Cambridge, UK.

Tillon, L., Aulagnier, S., 2014. Tree cavities used as bat roosts in a European temperate lowland sub-Atlantic forest. Acta Chiropt. 16, 359-368.

Tjørve, E., 2010. How to resolve the SLOSS debate: Lessons from species-diversity models. J. Theor. Biol. 264, 604-612.

Tomppo, E., Gschwantner, T., Lawrence, M., Mc Roberts, R.E., 2010. National forest inventories. Pathways for common reporting. Springer Science, Heidelberg, Allemagne.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P., Verschelde, P., 2009. When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. For. Ecol. Manag. 258, 425-435.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144, 441-450.

Winter, S., Begehold, H., Herrmann, M., Lüderitz, M., Möller, G., Rzanny, M., Flade, M., 2015a. Praxishandbuch - Naturschutz im Buchenwald. Ministerium für Ländliche Entwicklung, Umwelt und Landwirtschaft des Landes Brandenburg, Land Brandenburg.

Winter, S., Borrass, L., Geitzenauer, M., Blondet, M., Breibeck, R., Weiss, G., Winkel, G., 2014. The impact of Natura 2000 on forest management: a socio-ecological analysis in the continental region of the European Union. Biodivers. Conserv. 23, 3451-3482.

Winter, S., Chirici, G., McRoberts, R.E., Hauk, E., Tomppo, E., 2008. Possibilities for harmonizing national forest inventory data for use in forest biodiversity assessments. Forestry 81, 33-44.

Winter, S., Flade, M., Schumacher, H., Kerstan, E., Möller, G., 2005. The importance of near-natural stand structures for the biocoenosis of lowland beech forests. For. Snow Landsc. Res. 79, 127-144.

Winter, S., Höfler, J., Michel, A.K., Böck, A., Ankerst, D.P., 2015b. Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. European Journal of Forest Research 134, 335-347.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manag. 255, 1251-1261.

Wolters, V., Bengtsson, J., Zaitsev, A.S., 2006. Relationship among the species richness of different taxa. Ecology 87, 1886-1895.

2.2. Quantifier l'effet observateur : "Strong observer effect on tree microhabitats inventories: a case study in a French lowland forest" – Paillet et al. Ecol. Ind. (2015).

Ecological Indicators 49 (2015) 14–23

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest

Yoan Paillet*, Pauline Coutadeur, Aurélie Vuidot, Frédéric Archaux, Frédéric Gosselin

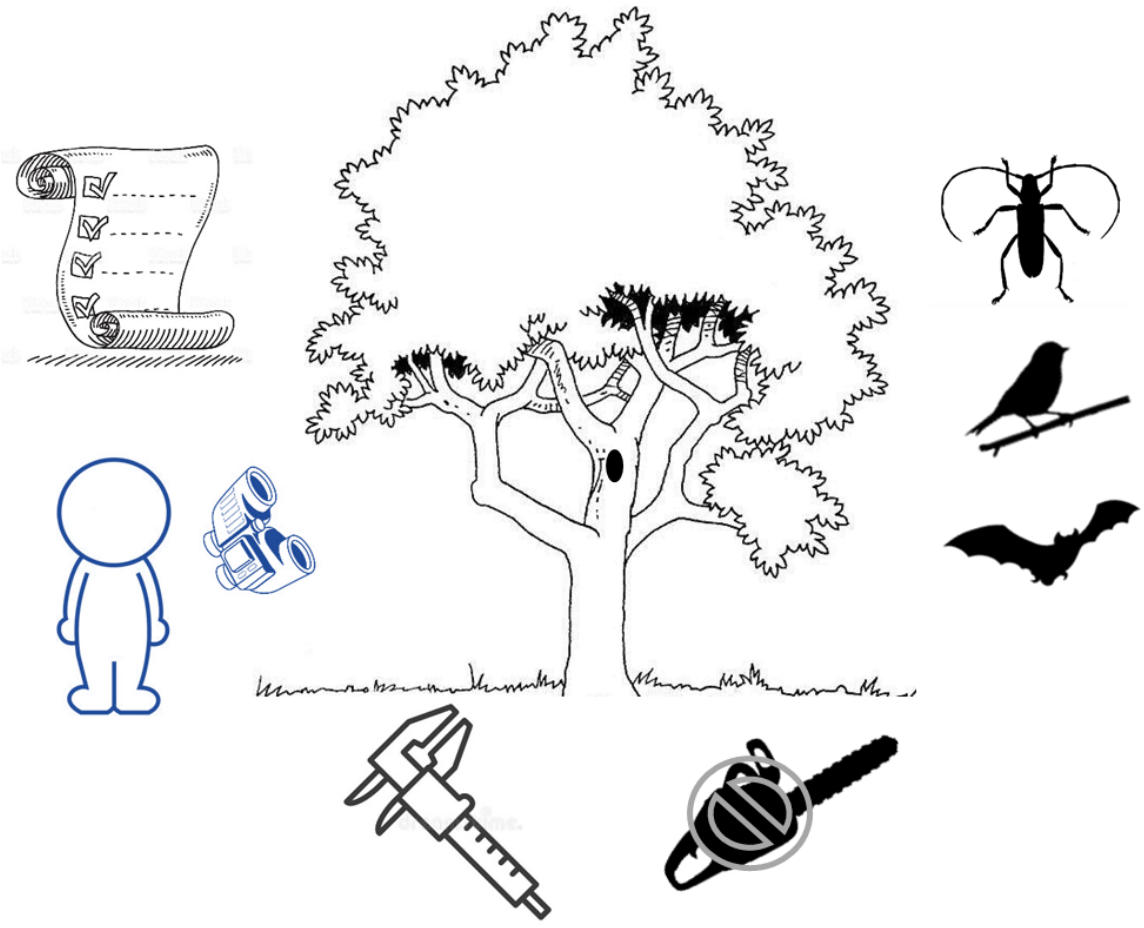
Résumé

La validation d'indicateurs de biodiversité requiert une analyse de leur applicabilité, de leur domaine de validité et du niveau de correlation avec la biodiversité qu'ils sont censés mesurer. Dans ce processus, évaluer la magnitude de l'effet observateur apparait comme une étape essentielle, en particulier lorsque des non-spécialistes sont impliqués dans les relevés. Les microhabitats des arbres – cavités de pics, fentes et caractéristiques de l'écorce – sont réputés faciles à inventorier par des non-spécialistes, car leur observation ne requiert pas de connaissances préalables en foresterie ou en écologie. Nous avons ainsi quantifié les probabilités de vraies et fausses détections positives par différents observateurs pendant des inventaires.

Dans deux placettes de 0.5 ha situées dans une réserve forestière n'ayant pas connu d'exploitation depuis au moins 150 ans, 14 observateurs avec différentes sensibilités ont inventorié les microhabitats sur 106 chênes (*Quercus petraea* et *Quercus robur*) et hêtres (*Fagus sylvatica*). Nous avons utilisé des statistiques paramétriques et Bayésiennes pour comparer ces observations avec les résultats d'un inventaire indépendant.

Le nombre moyen de microhabitats relevé par arbre varie largement entre les observateurs – entre 1.4 et 3 microhabitats par arbre. Seulement cinq observateurs ont relevé un nombre moyen de microhabitats statistiquement comparable au relevé de référence. La probabilité de détection variait également entre les observateurs pour chaque microhabitat (de 0 à 1), de même que la probabilité de fausse détection positive (de 0 à 0.7). Ces résultats montrent que les microhabitats sont particulièrement sensibles à l'effet observateur.

Un tel effet questionne l'utilité des microhabitats comme indicateurs de biodiversité. Si des inventaires de microhabitats doivent être entrepris, nous recommandons de contrôler les effets observateurs : (i) en définissant des procédures standardisées et en multipliant le nombre de sessions d'entrainement et de standardisation pour les observateurs ; (ii) en inventoriant les microhabitats à deux observateurs à chaque fois que possible (l'efficacité de cette méthode doit cependant être testée) ; (iii) en organisant le travail de terrain de manière à ce que les modalités d'intérêt ne soient pas confondues avec un effet observateur ; (iv) en intégrant les profiles des observateurs dans les modèles utilisés pour les analyses statistiques des relevés.



Strong observer effect on tree microhabitats inventories: a case study in a French lowland forest

Yoan Paillet*, Pauline Coutadeur, Aurélie Vuidot, Frédéric Archaux, Frédéric Gosselin

Irstea, UR EFNO, Nogent-sur-Vernisson
Address: Domaine des Barres, 45290 Nogent-sur-Vernisson, France
*corresponding author: yoan.paillet@irstea.fr

Abstract

Validating biodiversity indicators requires an analysis of their applicability, their range of validity and their degree of correlation with the biodiversity they are supposed to represent. In this process, assessing the magnitude of observer effect is an essential step, especially if non-specialist observers are involved. Tree microhabitats – woodpecker cavities, cracks and bark characteristics – are reputed to be easily detected by non-specialists as microhabitat observation does not require prior forestry or ecology knowledge. We therefore quantified the probabilities of true and false positive detections made by observers during inventories.

Within two 0.5ha plots in a forest reserve that has not been harvested for at least 150 years, 14 observers with various backgrounds visually inventoried microhabitats on 106 oak (*Quercus petraea and Q. robur)* and beech (*Fagus sylvatica*) trees. We used parametric and Bayesian statistics to compare these observers' recorded observations with results from an independent census.

The mean number of microhabitats per tree varied widely among observers – from 1.4 to over 3. Only five observers reported a mean number of microhabitats per tree that was statistically equivalent to the reference census. The probability of true detection also varied among observers for each microhabitat (from to 0 to 1) as did the probability of false positive detection (from 0 to 0.7). These results show that microhabitat inventories are particularly prone to observer effects.

Such strong observer effects weaken the usefulness of microhabitats as biodiversity indicators. If microhabitat inventories are to be developed, we recommend controlling for observer effects by (i) defining standard operating procedures and multiplying the number of observer training sessions and of consensual standardisation censuses; (ii) using pairs of observers to record microhabitats whenever possible (though the efficiency of this method remains to be tested); (iii) planning fieldwork so that the factors of interest are not confused with observer effects; and (iv) integrating observer profiles into the statistical models used to analyse the data.

Keywords: data quality, tree microhabitats, observer effect, detectability, Bayesian analysis

1. Introduction

Quality assurance is an integral part of the production process in most companies. Through the quality control process, the company insures that its products consistently fulfil a standardised set of quality and safety requirements, notably by establishing standard operating procedures. In ecology, such processes are rarely mentioned, except in long-term monitoring networks where high standards of quality assurance are applied (*e.g.* Allegrini et al., 2009; Ferretti, 2013 for forest monitoring). However, high-quality data is crucial to minimising noise and avoiding biases such as over- or under-estimations of species richness (Allegrini et al., 2009; Archaux et al., 2006). Among the possible sources of noise, observer effect has frequently been pinpointed, especially for data that rely on observation (Ahrends et al., 2011; Larjavaara and Muller-Landau, 2013). Indeed, observer effect has been identified as an important source of variation in ground flora surveys (Archaux et al., 2006; Gotfryd and Hansell, 1985) and bird censuses (Manu and Cresswell, 2007; Riffell and Riffell, 2002; Venier et al., 2012), but also in forest health assessment (Innes, 1988; Strand, 1996; Vales and Bunnell, 1988) or for estimations of classical forest measurements such as tree height (Ferretti et al., 2013; Larjavaara and Muller-Landau, 2013).

Even if observer effect can – and most of the time should – be included in statistical models explaining ecological patterns and processes, measures to limit it should first be taken before conducting any assessment. To be validated as relevant, an ecological indicator should have a limited observer effect, *i.e.* repeatability and solid confidence in estimations are mandatory (Sutherland et al., 2004). Several authors have recently proposed using tree microhabitats to explain biodiversity differences between managed and unmanaged forests (Michel and Winter, 2009; Vuidot et al., 2011) since these microhabitats appear to correlate with at least some components of biodiversity (Regnery et al., 2013a; Winter and Möller, 2008). In addition, microhabitat inventories are reputed to be easily performed by non-specialists as microhabitat observation does not require prior forestry or ecology knowledge (Regnery et al., 2013a). Yet as the quality of ecological data has been shown to depend on former field experience of the observers, a formal field test is warranted to validate the assertion that microhabitats can be monitored by the general public, *e.g.* through citizen science programs (see *e.g.* Butt et al., 2013; Kendall et al., 1996; Scott and Hallam, 2003).

In a broad sense, microhabitats are defined as small substrates used by certain species or groups of species to grow, nest or forage (*e.g.* numerous bryophytes preferentially grow on deadwood logs, Fenton and Bergeron, 2008). The term "microhabitat" hence encompasses various forest features and authors often differ in what they include in this category. Here, we have adopted a more restrictive definition which includes only microhabitats linked to living trees and snags (cavities, cracks and bark characteristics).

To validate tree microhabitats (hereafter referred to as "microhabitats") as indicators of biodiversity, one of the first steps is to assess the potential observer effect associated to their identification (Regnery et al., 2013b; Vuidot et al., 2011). Observer effect can vary according to observer skill or observation conditions. Several authors have pointed out the importance of training and observer experience as well as census duration (Ahrends et al., 2011; Archaux et al., 2006; Chen et al., 2009).

We hypothesized that observer identity, experience and training, as well as census duration, would all have an effect on the accuracy of microhabitat inventories. In other words, we aimed at testing whether microhabitat inventories done by either experienced or non-experienced observers were sensitive to observer effect. We quantified these effects and provided recommendations to help researchers and practitioners reduce observer effect in future studies.

2. Materials and methods

2.1. Study site descriptions and plot selection

We selected two 0.5ha (100x50m) plots located inside strict forest reserves near Fontainebleau, France (48°24'N, 2°42'E). These forest reserves have not been managed for at least 150 years and present certain characteristics of old-growth forests (Koop and Hilgen, 1987; Pontailler et al., 1997), particularly different tree microhabitat types. The stands are composed of two oak species (*Quercus robur* L. and *Q. petraea* Liebl.) and beech (*Fagus sylvatica* L.). Both plots have similar topographic and stand structure characteristics: they are both flat, high forest stands with large (mean diameter at breast height +/- SD = 70 +/- 44cm) and tall trees (dominant height = 30m), and low density (100 stems per hectare). Understory vegetation was absent from the plots, so that all observers had clear views of the trees. For these reasons, we assumed that plot effect was negligible.

In the two plots, the microhabitats present on all trees with a Diameter at Breast Height (DBH) > 30cm (50 and 56 trees for plots 1 and 2 respectively) were inventoried. We used a list of 28 microhabitats adapted from Vuidot et al. (2011, Tableau 8).The trees differed considerably in terms of the types and number of microhabitats they hosted.

2.2. Reference census

Before conducting the observer test, a reference census was conducted by three observers (P.C., H. Martin and Y.P.). Each observer first independently checked each tree visually without binoculars for 3 minutes. Then, the three observers worked together to draw up a consensual list of the microhabitats observed on each tree. In case of disagreement, the final choice was made after voting. We assumed this list to be complete, and used it as a reference for the subsequent observer effect test. In preliminary analyses (results not shown), we tested the possibility that some microhabitats had been overlooked during the reference census but detected by some of the observers during the observer test. However, model estimates remained very close to those obtained when assuming exhaustiveness of the reference census, thus suggesting very few omissions in the reference lists.

2.3. Observer effect test

Fourteen volunteers participated in the test. They independently observed all the selected trees in the two plots and visually assessed the presence of the 28 microhabitat types (Tableau 8). The 14 observers were of different backgrounds (5 researchers in forest ecology, 2 foresters, 6 Master's students in ecology, and 1 administrative staff member) and genders (8 females and 6 males). Six were considered "experienced" since they had conducted a similar test the year before and/or were used to such inventories; the others were considered to be inexperienced as they just discovered the protocol during the test. As microhabitat inventories are reputed to be easily performed by non-specialists (Regnery et al., 2013a), we assumed that testing observer effects with a team composed of people with various backgrounds instead of professional foresters only would help verify this statement. Therefore, for the present observer effect test, we reproduced general conditions (limited duration, one single observer, various degrees of professionalism) applied for microhabitats inventories in routine monitoring.

We organised three sessions during early spring when the trees were bare and the microhabitats more easily observable (March 24th and 26th, and April 12th, 2010). The weather conditions varied slightly among the sessions (mostly sunny with mild temperatures around 15°C) and few drops of rain fell during the second session. However, we assumed that this change did not affect the quality of the observations. To assess the effects of so-called "familiarity" on observation quality, we noted the order in which the two plots were observed during each session (*i.e.* in the morning or in the afternoon). Observers were considered familiar with the protocol when the inventories were done in the afternoon.

Microhabitat type	Proportion microhabitat bearing trees (%)
1. Presence of a crown skeleton (snags only)	3.8
2. Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown	12.3
3. Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown	0.9
4. >50% of dead crown: one or more main branches are dead. The living crown seems to be <50% of the former total crown	0.0
5. Broken stem: the primary crown is totally absent with or without the presence of a secondary crown. Main parts of the tree stem are already dead and decomposing	2.8
6. Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch has resulted in severe damage to the main stem	2.8
7. Splintered stem: splitting-has resulted in numerous slabs (minimum 5) of wood >50 cm long	0.0
8. Conks of fungi. Fruiting bodies, diameter > 5cm.	6.6
9. Conks of fungi. Equal to or more than 3 fruiting bodies >5 cm in diameter	0.9
10. Conks of fungi occurring in 10 cm long cascades of small fruiting bodies	4.7
11. Woodpecker cavities with >2 cm aperture.	7.5
12. Non-woodpecker cavities with >5cm aperture: formed after injury, branch fall.	53.8
13. Cavity string: at least three woodpecker cavities on a same stem with a maximum distance of two meters between two cavity entrances	3.8
14. Deep stem cavities: a tubular cavity in the base of the tree.	7.5
15. Deep stem cavities: a tubular cavity in the base of the tree with mould.	0.9
16. Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	0.0
17. Cracks: cleft in the sapwood >25 cm long along the stem and at least 2 cm deep in the sapwood	34.9
18. Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 cm × 5 cm × 2 cm	42.5
19. Bark pocket with mould: same structure and size as 17. but with mould	5.7
20. Bark loss: patches with bark loss of at least 5 cm × 5 cm mainly caused by injuries sustained from felling or natural falling of other trees	84.0
21. Bark burst: black burst of bark often with resin indicating injury/disease	0.9
22. Recent wood injury	2.8
23. Canker: proliferation of cell growth; irregular cellular growth on stems or branches, caused by bark-inhabiting fungi, viruses and bacteria. Areas of canker >10 cm in diameter were recorded	8.5
24. Witch broom: dense agglomeration of branches from a parasite or epicormic branching.	5.3
25. Heavy sap or resin: fresh, heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size	0.9
26. Sap or resin drop: Only a few sap or resin drops indicating a minor injury	0.9
27. Bryophytes developed on >50% of the base, trunk or branch area (noted separately)	Base: 37.7; trunk: 12.3; branches: 8.5
28. Ivy growing on >50% of the base, trunk or branch area (noted separately)	Base: 0.0; trunk: 0.9; branches: 0.9

Tableau 8 : List of the 28 tree microhabitats used for the observer effect test and proportion of trees occupied by each microhabitat (based on the reference census). Microhabitats 1 to 7 represent general tree features while microhabitats 8 to 28 describe more specific tree structures.

Following recommendations by previous studies (Archaux et al., 2009; Archaux et al., 2006; Ferretti et al., 2013), several constraints were applied to the volunteers in order to limit the variations inherent to this type of experiment. These measures were aimed at standardizing the observation protocol as much as possible (Ferretti et al., 2013):

- each observer was provided with a sheet detailing the complete list of 28 microhabitats with a short description of each microhabitat (Tableau 8) and drawings issued by Table 2 in Winter and Möller (2008, pp. 1254-1255);

- prior to the test, we presented the list of microhabitats to the observers and trained them on five trees chosen outside of the test plots once before the morning session;
- observation time was roughly limited to 3 minutes per tree. In practice, we limited the total observation time to 2.5 hours per plot and noted how long it took each observer to finish the census for each plot (total duration of census per plot).

2.4. Statistical analyses

We considered two response variables in our analyses: "microhabitat number" was the number of different microhabitat types per tree, and "occurrence" corresponded to the presence of a given microhabitat type on a tree. All the tests were considered significant when the associated critical value (p) was less than 0.05, and marginally significant when $0.05<p<0.1$.

We processed the following analyses with the R software v. 2.15.2 (R Core Team, 2012). We modelled the response of microhabitat number to observer effect with generalized linear mixed models (GLMM, Bolker et al., 2009), using the lmer function in the lme4 R package. Indeed, GLMM can handle non-normally distributed data and incorporate random effects. Both aspects were important here: the number of microhabitats was count data for which a normal distribution was inappropriate, so we used a Poisson error distribution. Furthermore, since our sampling design was based on multiple surveys of the same trees within the two study plots, we included a Gaussian random "tree" effect to take this source of autocorrelation into account. Finally, we included an “observation” (*i.e.* a microhabitat on a given tree noted by a given observer) random effect to account for potential over-dispersion of the data (Elston et al., 2001). We tested the effect of observer identity on the number of microhabitats found per tree using a multi-comparison Tukey test (R package: multcomp, function: glht). The reference census was included as a supplementary observer to compare the microhabitat number for each observer to a single reference.

We also tested the effects of experience (experienced vs inexperienced), total duration of the census and familiarity (unfamiliar: census in the morning; familiar: census in the afternoon) on the number of microhabitats found per tree and occurrence of individual microhabitats that were present in more than 5% of the trees according to the reference census (14 of the 28 studied, including the three locations for bryophytes, Tableau 8). Poisson error distribution was used for the number of microhabitats per tree and binomial error distribution for occurrences. Experience, duration and familiarity were used as explanatory variables in three separate models, with observer identity as a random effect (in addition to the “tree” effect previously mentioned).

For microhabitat occurrence, we further estimated two types of probabilities:

- true detection probability (aka. detectability): probability of detecting a microhabitat that is present in the reference census;
- false positive detection probability: probability of recording as present a microhabitat that is absent in the reference census.

It should be noted that the true detection probability could have been influenced to some extent by the false positive detection probability: observers may not have actually detected a microhabitat reported by the reference census but instead, may have made an assessment error. Thus, the higher the false positive detection probability for a given observer, the higher the overestimation of the associated true detection probability.

We modelled the responses using Bayesian methods in the Winbugs software. One model was fitted to each of the 14 most common microhabitats. We based our modelling on the estimation of false positive probabilities and true detection. False positive detection probability (PF) was modelled for each tree i and each observer j as the addition of an observer fixed effect and a tree random effect on a logit scale as follows:

$$logit\left(PF\left[i, j\right]\right) = a_{PF}\left[i\right] + \beta_{PF}\left[j\right]$$

with a uniform prior between -5 and 5 for $a_{PF}[i]$ and a scaled normal distribution for $\beta_{PF}[j]$, with a standard deviation σ_{PF}.

The prior distribution of σ_{PF} was a uniform distribution between 0.1 and 10.

A similar setting was chosen for true detection probability (PT). The overall likelihood linking these parameters to the observed reference values involved two series of data: the observed presence/absence of the microhabitat by observer i on the j[th] tree, $Y[i, j]$, and the reference data for the j[th] tree, $Y_{cons}[j]$. $Y_{cons}[j]$ was considered exact and therefore did not have a probability distribution. The likelihood of $Y[i, j]$ actually depended on the value of $Y_{cons}[j]$, as follows:

- When $Y_{cons}[j]=1$, the probability of $Y[i, j]=1$ was the sum of the true detection probability (the observer correctly detected the microhabitat) and the product of the non-detection probability and the false positive detection probability – corresponding to the case where the observer had not detected the correct microhabitat but had (wrongly) detected another one on the same tree.
- The probability of $Y[i, j]=0$ was simpler and corresponded to the case where the observer had not detected the microhabitat and had neither detected another one: that is, the product of the probability of non-detection and of that of false positive non-detection.

When $Y_{cons}[j]=0$, formulas were even simpler: the probability of $Y[i, j]=1$ was the probability of false positive detection and the probability of $Y[i, j]=0$ was 1 minus the probability of false positive detection.

This resulted in the following four formulas:

$$P(Y[i, j]=1|Y_{cons}[j]=1)=PT[i, j]+(1-PT[i, j])\,PF[i, j]$$

$$P(Y[i, j]=0|Y_{cons}[j]=1)=(1-PT[i, j])\,(1-PF[i, j])$$

$$P(Y[i, j]=1|Y_{cons}[j]=0)=PF[i, j]$$

$$P(Y[i, j]=0|Y_{cons}[j]=0)=(1-PF[i, j])$$

The models were run from R version: 2.15.2 (R Core Team, 2012) to Winbugs through the bugs function in the R package R2WinBUGS on three trajectories with a burn-in period of 1000, a total number of iterations of 10,000 and a thinning parameter of 10. Each of the resulting values for $a_{PF}[i]$ and $a_{PT}[i]$ was used to create a random bivariate value $c(a_{PF}[\tilde{i}], a_{PT}[\tilde{i}])$ by drawing a random observer $\tilde{i}$ among the 14 observers. The empirical variation of this vector was summarized by delimiting confidence regions – at the 30, 50, 70 and 95% levels – through the ellipse function (R package ellipse).

3. Results

3.1. Microhabitat number

Observer effect on microhabitat number was strong and between-observer differences revealed by multi-comparisons highlighted this effect (Figure 4): the number of observed microhabitats per tree ranged from 1.4 (obs. 10) to 3.2 (obs. 7). Based on multi-comparison tests, three groups could be identified: the ones who observed around 2 microhabitats per tree (obs. 10, 8, 14, 5, 12, 1, 11); those who observed around 2.5 microhabitats per tree (obs. 6, 3, 13, 2, 9, 4); and observer 7 who observed an elevated 3.2.

The reference census averaged 3.1 microhabitats per tree. Only observers 7, 4, 9, 2 and 13 reported significantly similar mean numbers of microhabitats per tree, and remarkably, only one of them was "experienced" (obs. 9). All the other observers were significantly below the value of the reference census (Figure 4).

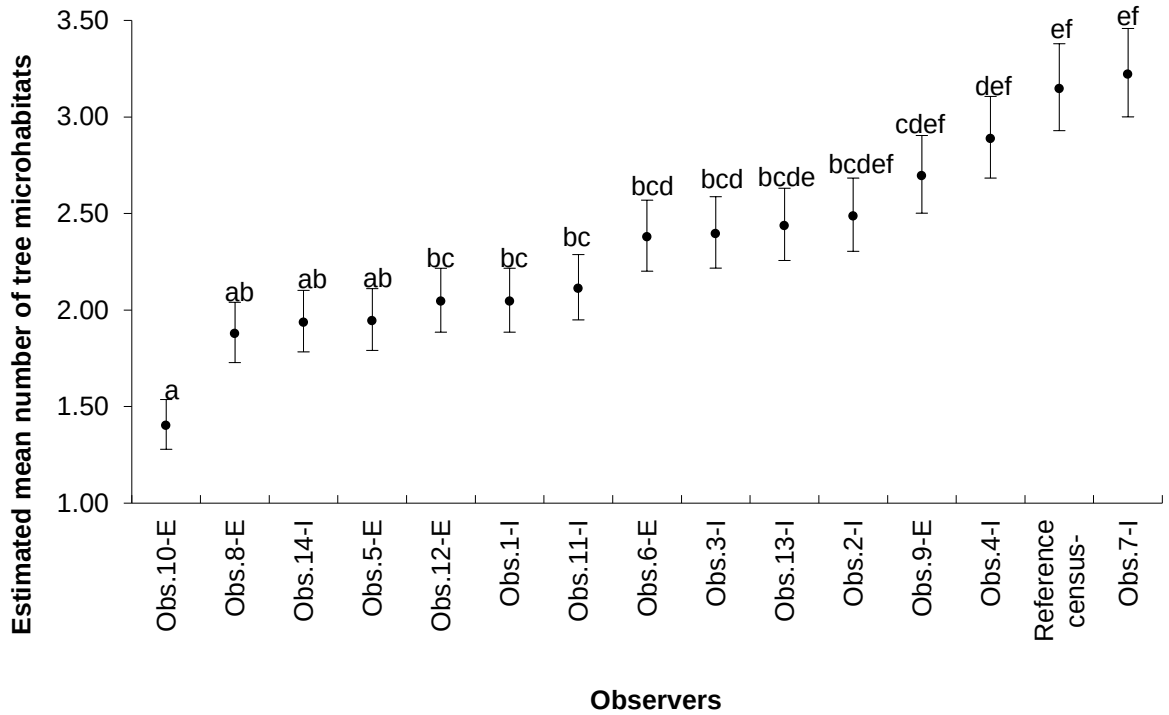


Figure 4 : Estimated number of tree microhabitats per observer in the two oak-beech plots in Fontainebleau (France, n=106 trees). Different letters indicate statistically different estimations between observers as assessed by a Tukey multi-comparison test on a general linear mixed-effects model. Letters "E" and "I" after observers' identifiers respectively refer to "Experienced" and "Inexperienced" observers.

3.2. Effects of experience, observation time and familiarity

Experienced observers who had already used the protocol tended to detect fewer microhabitats than inexperienced ones (mean +/- SE: 2.02 +/- 1.09 vs 2.41 +/- 1.09 respectively, see also Figure 4), but this result was only marginally significant (p=0.08, Tableau 9). At the individual microhabitat level, experience had a significant effect only on the occurrence of 10-25% deadcrown and bark pockets with mould (Tableau 10): inexperienced observers tended to detect more of these microhabitats (on 14.5% of the trees for deadcrown, and on 2.6% of the trees for bark pockets with mould) than experienced ones (resp. 4.3% and 0.6%) and the effect was strong.

Variables		Estimate	SE	p	
Experience	Intercept	0.702	0.090		
	Inexperienced	0.175	0.099	0.078	(*)
Duration	Intercept	0.883	0.079		
	Census duration	0.001	0.001	0.165	ns
Familiarity	Intercept	0.836	0.076		
	Unfamiliar	-0.067	0.034	0.047	*

*Tableau 9 : Effect of experience, observation time and familiarity with the protocol on the total number of observed microhabitats per tree. We used generalized linear models with Poisson error distributions and tree (n=106), observers (n=14) and observation (n=14x106=1484) as random effects. SE: standard error. *p<0.05; (*) p<0.1; ns: p>0.1*

Microhabitat type		Estimate	SE	p	
10-25% Deadcrown	Intercept	-3.102	0.472	0.000	***
	Inexperienced	1.329	0.5983	0.026	*
Conks of Fungi	Intercept	-8.710	1.335	0.000	***
	Inexperienced	-0.592	0.5913	0.317	ns
Woodpecker cavities	Intercept	-3.793	0.427	0.000	***
	Inexperienced	0.215	0.518	0.678	ns
Non-woodpecker cavities	Intercept	-1.347	0.574	0.019	*
	Inexperienced	-0.483	0.7251	0.505	ns
Deep stem cavities	Intercept	-9.791	1.605	0.000	***
	Inexperienced	0.378	0.5925	0.524	ns
Cracks	Intercept	-2.964	0.423	0.000	***
	Inexperienced	0.146	0.4809	0.761	ns
Bark pockets	Intercept	-1.436	0.509	0.005	**
	Inexperienced	0.104	0.648	0.873	ns
Bark pockets with mould	Intercept	-5.193	0.584	0.000	***
	Inexperienced	1.581	0.6829	0.021	*
Bark loss	Intercept	0.222	0.408	0.587	ns
	Inexperienced	0.570	0.4978	0.252	ns
Canker	Intercept	-5.149	0.548	0.000	***
	Inexperienced	0.018	0.49751	0.971	ns
Witch broom	Intercept	-5.399	0.478	0.000	***
	Inexperienced	0.446	0.5033	0.376	ns
Bryophytes (trunk base)	Intercept	-2.838	0.860	0.001	***
	Inexperienced	0.450	1.081	0.677	ns
Bryophytes (trunk)	Intercept	-3.926	0.621	0.000	***
	Inexperienced	-0.274	0.7097	0.700	ns
Bryophytes (branches)	Intercept	-4.124	0.683	0.000	***
	Inexperienced	0.480	0.8746	0.583	ns

*Tableau 10 : Effect of experience on the observations of microhabitats that occurred in more than 5% of the reference census. We used generalized linear models with Binomial error distributions and tree (n=106) and observers (n=14) as random effects. The general equation of the model is logit(P(x))=α + βx where P(x) is the probability of observation of the microhabitat, α the intercept of the model, β the slope, and x equals 0 for experienced observers and 1 for inexperienced observers. SE: standard error. *p<0.05; **p<0.01; ***p<0.001; ns: p>0.1*

Census duration had no significant effect on the mean number of microhabitats per tree recorded by the observers. At the individual microhabitat level, only detection of bark losses was influenced by duration (Tableau 11): the longer the census, the fewer bark losses were detected.

The number of observed microhabitats tended to increase with familiarity: after a first session in the morning, the observers tended to see more microhabitats in the afternoon; however, the magnitude of this effect was very low (mean +/- SE: 2.15 +/- 1.08 vs 2.30 +/- 1.08) and only slightly significant (p=0.047, Tableau 9). At the individual microhabitat level, familiarity with the protocol increased the detection of 10-25% deadcrown, non-woodpecker cavities, cracks and bark losses but only the latter showed a strongly significant and large effect (Tableau 12). Conversely, observers familiar with the protocol noted less often bryophytes cover either on trunk and trunk base than unfamiliar observers.

Microhabitat type		**Estimate**	**SE**	**p**	
10-25% Deadcrown	Intercept	-1.309	0.917	0.153	ns
	Duration	-0.009	0.008	0.212	ns
Conks of Fungi	Intercept	-10.747	1.903	<0.001	***
	Duration	0.015	0.012	0.222	ns
Woodpecker cavities	Intercept	-4.880	1.011	<0.001	***
	Duration	0.011	0.009	0.200	ns
Non-woodpecker cavities	Intercept	-1.475	0.968	0.128	ns
	Duration	-0.001	0.008	0.866	ns
Deep stem cavities	Intercept	-10.893	2.174	<0.001	***
	Duration	0.012	0.013	0.379	ns
Cracks	Intercept	-2.559	0.946	0.007	**
	Duration	-0.003	0.008	0.715	ns
Bark pockets	Intercept	-0.973	0.889	0.274	ns
	Duration	-0.004	0.008	0.622	ns
Bark pockets with mould	Intercept	-4.118	1.380	0.003	**
	Duration	-0.001	0.012	0.904	ns
Bark loss	Intercept	2.975	0.835	<0.001	***
	Duration	-0.022	0.007	0.002	**
Canker	Intercept	-6.732	1.088	<0.001	***
	Duration	0.014	0.009	0.109	ns
Witch broom	Intercept	-6.712	1.210	<0.001	***
	Duration	0.014	0.010	0.163	ns
Bryophytes (trunk base)	Intercept	-4.445	1.361	0.001	**
	Duration	0.017	0.011	0.123	ns
Bryophytes (trunk)	Intercept	-4.901	1.348	<0.001	***
	Duration	0.007	0.012	0.521	ns
Bryophytes (branches)	Intercept	-3.305	1.425	0.020	*
	Duration	-0.010	0.012	0.425	ns

*Tableau 11 : Effect of total duration on the observations of microhabitats that occurred in more than 5% of the reference census. We used generalized linear models with Binomial error distributions and tree (n=106) and observers (n=14) as random effects. The general equation of the model is logit(P(x))=α + βx where P(x) is the probability of observation of the microhabitat, α the intercept of the model, β the slope and x the duration. SE: standard error. *p<0.05; **p<0.01; ***p<0.001; ns: p>0.1*

It should be noted however that many of the analyses done at the individual microhabitat level provided very noisy estimations (and consequently unreliable tests) due to the scarcity of the microhabitats studied (see Tableau 9).

Microhabitat type		Estimate	SE	p	
10-25% Deadcrown	Intercept	-2.204	0.360	<0.001	***
	Unfamiliar	-0.279	0.165	0.092	(*)
Conks of Fungi	Intercept	-9.420	1.349	<0.001	***
	Unfamiliar	0.563	0.447	0.207	ns
Woodpecker cavities	Intercept	-3.559	0.317	<0.001	***
	Unfamiliar	-0.237	0.234	0.311	ns
Non-woodpecker cavities	Intercept	-1.496	0.412	<0.001	***
	Unfamiliar	-0.280	0.151	0.063	(*)
Deep stem cavities	Intercept	-9.883	1.607	<0.001	***
	Unfamiliar	0.412	0.460	0.371	ns
Cracks	Intercept	-2.736	0.334	<0.001	***
	Unfamiliar	-0.318	0.186	0.086	(*)
Bark pockets	Intercept	-1.268	0.356	<0.001	***
	Unfamiliar	-0.221	0.139	0.111	ns
Bark pockets with mould	Intercept	-4.179	0.459	<0.001	***
	Unfamiliar	-0.203	0.243	0.402	ns
Bark loss	Intercept	0.904	0.317	0.004	**
	Unfamiliar	-0.691	0.140	<0.001	***
Canker	Intercept	-5.156	0.481	<0.001	***
	Unfamiliar	0.084	0.294	0.776	ns
Witch broom	Intercept	-5.207	0.408	<0.001	***
	Unfamiliar	0.116	0.377	0.759	ns
Bryophytes (trunk base)	Intercept	-2.956	0.617	<0.001	***
	Unfamiliar	0.681	0.210	0.001	**
Bryophytes (trunk)	Intercept	-4.454	0.504	<0.001	***
	Unfamiliar	0.626	0.263	0.017	*
Bryophytes (branches)	Intercept	-4.422	0.510	<0.001	***
	Unfamiliar	0.068	0.303	0.823	ns

*Tableau 12 : Effect of familiarity on the observations of microhabitats that occurred in more than 5% of the reference census. We used generalized linear models with Binomial error distributions and tree (n=106) and observers (n=14) as random effects. The general equation of the model is logit(P(x))=α + βx, where P(x) is the probability of observation of the microhabitat, α the intercept of the model, β the estimate of the slope, and x equals 0 for observers who were familiar with the protocol and 1 for observers who were unfamiliar. SE: standard error. ***p<0.001; **p<0.01; *p<0.05; (*)p<0.1; ns: p>0.1.*

3.3. True and false detection probabilities (Figure 5)

All 14 microhabitat types analysed showed low levels of conformity to the reference census but this varied by microhabitat.

Dead crown (10-25%) was detected in only 15% of the cases with wide variations among observers and was incorrectly detected on average in 10% of the cases, up to 90% for one observer. For conks, cankers and witch brooms, observation patterns were similar: mean levels of detection were 40 to 50% and levels of false detection were less than 5%.

Woodpecker cavities and deep stem cavities were detected in 40% of the cases but with wide variations among observers. However, woodpecker cavities were incorrectly detected in only 10% of the cases; detection probability for deep stem cavities was even lower. Non-woodpecker cavities were detected in 20% of the cases with extremely wide variations - from 0 to 90%. False positive detection probability averaged 10% and varied from 0 to 50%.

Cracks were detected in 10% of the cases with a maximum value of only 80%. Mean false positive detection rates remained low (peaking at 30%) but with wide variations. Bark pockets were poorly detected (10%) with wide variations (0-90%) and incorrectly detected in 10% of the cases with variations reaching 80%. Bark pockets with mould were detected in 25% of the cases with wide variations from the mean. They were incorrectly detected in 15% of the cases. Bark losses were relatively well detected with a mean of 60% but detection probability varied widely. False positive detection rates were as high as for bark pockets (mean 20% with variations to 80%).

Bryophytes on the base of the trunk (height < 1m) were poorly detected (20%) with wide variations, and highly incorrectly detected with the maximum reaching 80%. Bryophytes present on the trunk above 1m were detected in 60% of the cases and rarely incorrectly detected, but the variations were very wide. Bryophytes present on branches were detected in 30% of the cases and were less incorrectly detected than those on the base of the trunk (maximum 25%).

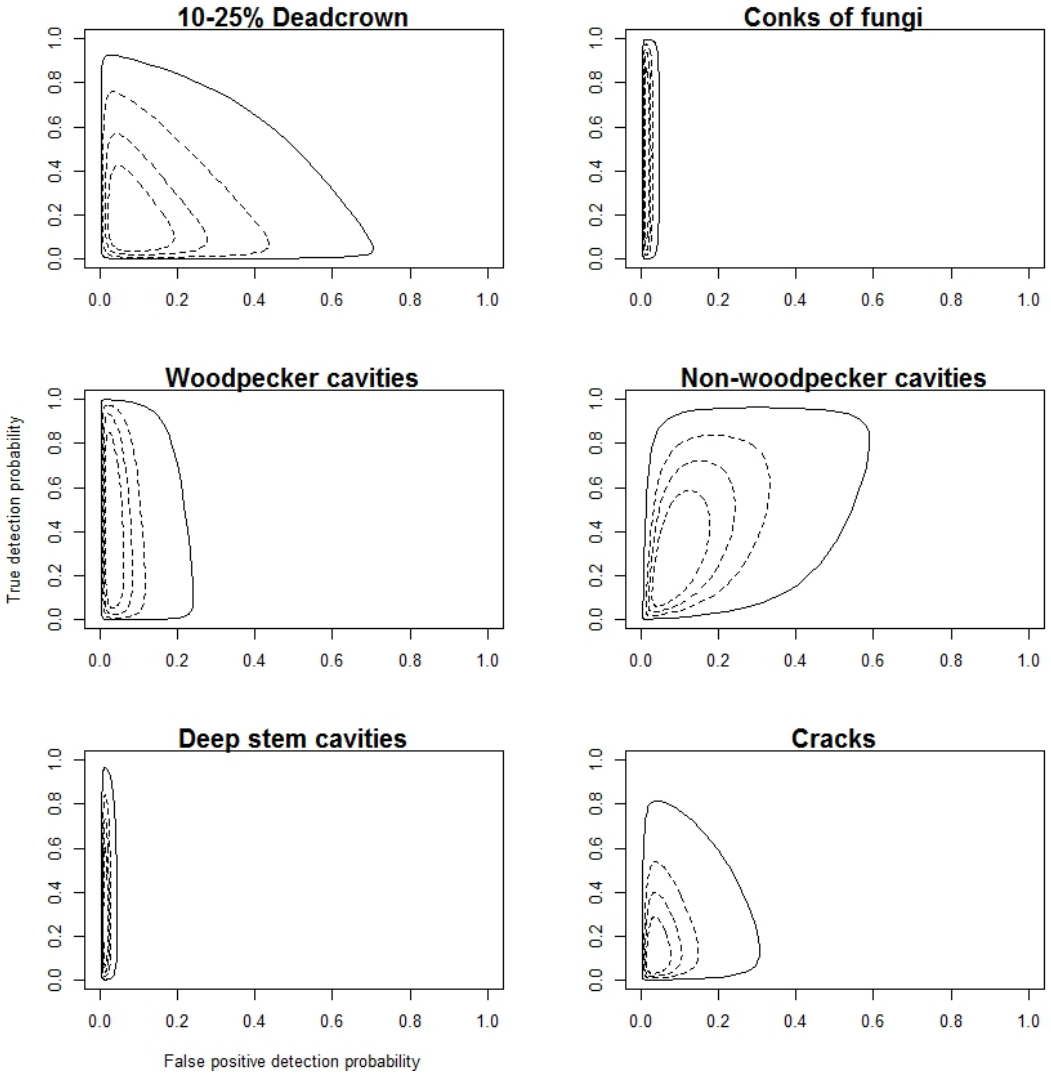


Figure 5 : Estimated probabilities of true and false positive detections in the two oak-beech plots in Fontainebleau (France, n=106 trees, 14 observers) on tree microhabitats occurring in more than 5% of the reference census. The two probabilities are defined as follows: (i) true detection probability (aka. detectability): probability of detecting a microhabitat that is present in the reference census; (ii) false positive detection probability: probability of recording as present a microhabitat that is absent in the reference census. Solid ellipsoids represent 95% confidence intervals and dashed ellipsoids represent 70, 50 and 30% confidence intervals.

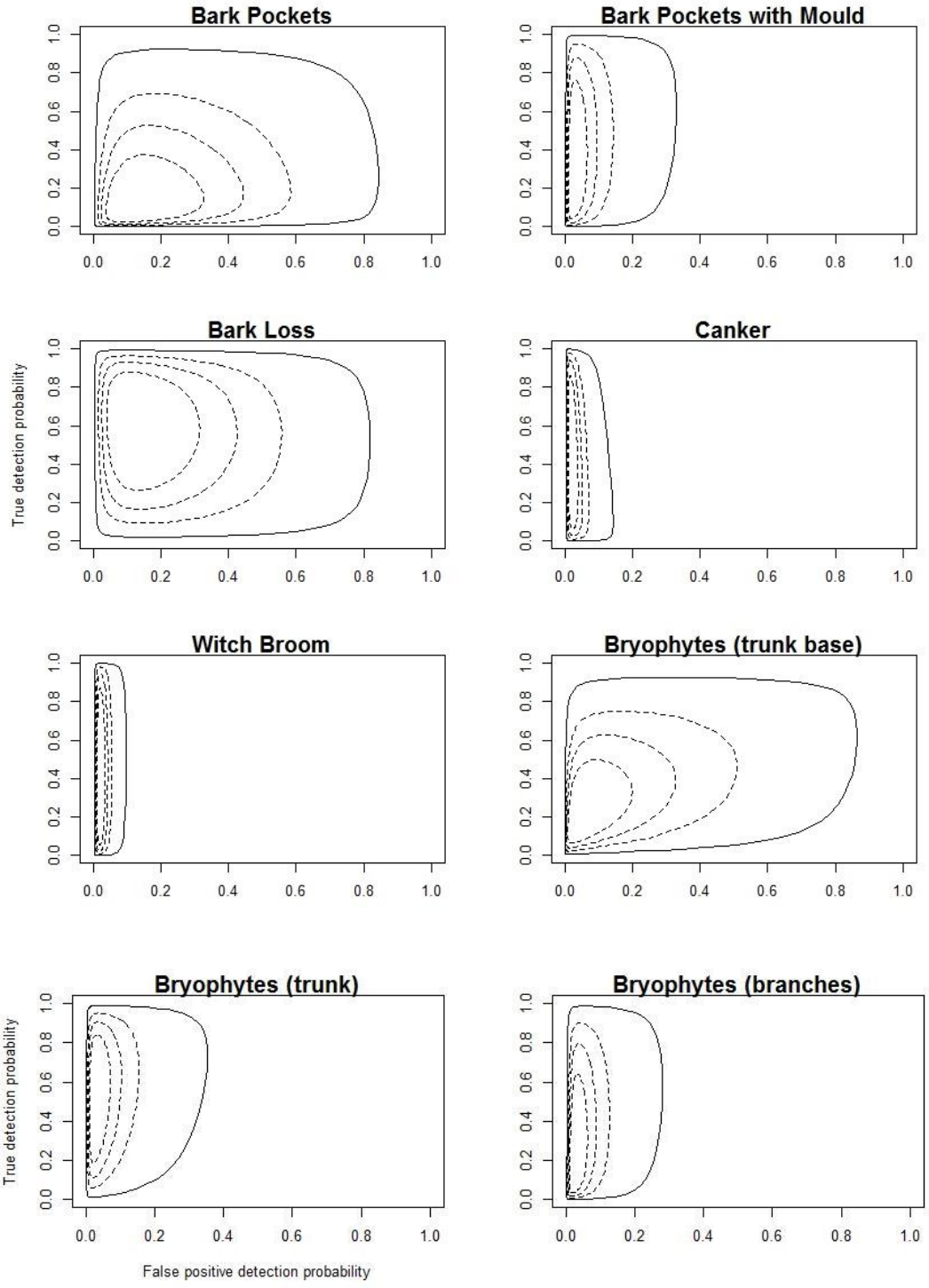


Figure 5 (continued)

4. Discussion

4.1. Why is observer effect on tree microhabitats so strong?

Observer effect may strongly affect the results of a study by introducing a bias in the estimation of the targeted parameters; however, this is generally overlooked in scientific studies (Archaux et al., 2009; Chen et al., 2009; but see Ferretti and Fischer, 2013). Observer effect has multiple causes, not only related to the skills and experience of the observers (Manu and Cresswell, 2007), but also to multiple environmental and contextual factors that may have a non-negligible effect on detectability, *e.g.* sampling area and census duration in plant studies (Archaux et al., 2007; Archaux et al., 2006; Chen et al., 2009), presence of vegetation or background noise in bird point counts (Pacifici et al., 2008). Here, we have shown that observers largely disagreed on the presence and the number of microhabitats on a given tree. Despite the impressively low levels of true detection and high levels of false positive detection, such rates are not uncommon in biodiversity and forest studies. For example, Pacifici et al. (2008) showed that bird detectability may vary from 3 to 99% depending on the species and the conditions; Chen et al. (2009) showed that detectability of forest trees and shrubs varied from 9 to 34%; Larjavaara and Muller-Landau (2013) showed that, depending on the method, the height of a given tree may be overestimated by more than 100%.

Although causes of bias in the previous examples have been attributed to various biotic and abiotic effects, our study under controlled homogeneous conditions reveals that observer identity was probably the main source of variation. We also found that experience and familiarity had only marginal effects on the total number of microhabitats detected, contrary to studies on more specialized objects such as vascular plants, for which the effect is highly significant (Ahrends et al., 2011; Archaux, 2009). At the individual microhabitat level, experience affected the detection of only two microhabitats out of 14 studied, while total duration affected only one. Concerning familiarity, only bark losses and bryophyte cover (trunk base and trunk) showed a significant influence. Familiarity could be interpreted as a combination of increasing self-confidence and true observation capacities, that could both modify detection probabilities. Familiarity may hence improve detection but also increase errors due to over-confidence. It should also be noted that the way we defined familiarity may have influenced our results: different light conditions between morning and afternoon may have influenced censuses towards better detections in the afternoon. However, these results have to be interpreted carefully as the relatively small size of our sample concerning rare microhabitats results in unreliable model estimations.

Finally, we hypothesize that the main source of errors in our study was probably the misunderstanding of the definitions of the microhabitat types (Archaux et al., 2007; Chen et al., 2009), the misidentification and confusion between microhabitat types, and the differences in evaluating the threshold values to take certain microhabitats into account (*e.g.* dead crown percentage). In addition, the reference census was conducted with three observers to ensure exhaustiveness and consensus. The systematic bias towards finding more microhabitats than the single test observers was due to the fact that the reference was performed by multiple observers while the test was performed individually. Another solution would have been to agree on a reference list for each tree with all observers together after the test (see *e.g.* Archaux, 2009), but in the present case, this would have further reduced the time of the test and the actual number of trees observed and finally lead to decrease the statistical power of our analyses. To conclude, we were aware that our method for establishing the reference list was not ideal but represented a pragmatic compromise regarding the conditions of the test.

4.2. Can we limit observer effects on microhabitat inventories?

For this study, we controlled several factors that could potentially influence the relevance of microhabitat inventories. We provided the observers with descriptions and drawings of the microhabitats to be observed as a form of standard operating procedure (Cline and Burkman, 1989). However, as misidentification of microhabitats seems to remain among observers, more detailed

descriptions should probably be provided in further tests. We standardized the observation time per tree to 3 minutes, the maximum time allocated to such observations in routine monitoring. As a consequence, we could not detect any time effect. Conversely, familiarity tended to increase the total number of microhabitats observed and the detection of certain types, although quite marginally. Contrary to our expectations, experience tended to reduce the number of microhabitats observed, by especially affecting 10-25% deadcrown and bark pockets with mould. This finding supports including training in protocols to improve detection probabilities (Ahrends et al., 2011). Conversely, routine may also lead to overlooking certain microhabitats through too quick assessments (see Archaux, 2009 for a similar conclusion on plant censuses). However, the effect we found in our study of tree microhabitats seems rather small, and the effects of experience are unclear. It could therefore not be totally excluded that such mistakes are more pronounced for inexperienced observers and that further study with trained observers only would strongly limit inconsistencies in observations. Further research is thus needed to disentangle these effects.

In addition, observer effect on total detection may mask compensations between microhabitat types. For example, inexperienced observer 7 detected a similar (even slightly higher) number of microhabitat types than the reference census, but that is because this observer noted bryophytes on all trees without apparently taking into account the cover threshold of 50% in the microhabitat definition. Despite this peculiarity, no further systematic compensation scheme could be detected through our analyses. Once again, such effect was probably also due to the fact that some observers did not have any prior knowledge in forestry as we wanted to test observer effect on a panel of people with diverse origins.

Various ways to limit observer effects have been documented and some that may be effective in the case of microhabitats should be mentioned. First, standard operating procedures and clear protocol should be provided to observers. Then, calibration training and a common consensual census at the beginning of the sampling sessions appear to be essential to ensure that the protocol is well understood and that the microhabitat types – and more generally the objects studied – are correctly noted (Allegrini et al., 2009; Archaux et al., 2009). Second, working in teams has shown to improve detectability and exhaustiveness, notably for vascular plants (Archaux et al., 2009). We intentionally carried out our test with individual observers rather than teams (2 observers working together, for example) as we wanted to reproduce the conditions in which microhabitats are currently inventoried in routine fieldwork. Many different ways to combine observations have been described in the literature (*e.g.* Dawson and Efford, 2009; Nichols et al., 2000):

- two observers work together and exchange ideas on the observed microhabitats to obtain a consensual census;
- one first observer notes all the microhabitats seen, then a second observer confirms or rejects the detections made by the first observer and adds his/her own observations to those detected by the first observer. Observers alternate primary and secondary roles during the course of the survey;
- first, observer skills are assessed, then experienced observers are teamed up with novices; experienced observers change teams during the field campaign whenever possible.
- two observers note the microhabitats independently and an observer effect is estimated in the data analyses;

In terms of tree microhabitat observation, the systematic use of binoculars would probably improve observation accuracy but this expected positive effect remains to be tested. Ultimately, observers could be asked to note both microhabitat presence and its estimated dimensions (or abundance-dominance). This would partly remove the problem related to thresholds in the definition of microhabitats, but would necessitate complex data analyses which require further testing.

Given our results, and in view of the actual link between certain microhabitats and biodiversity (Regnery et al., 2013a), another solution would be to simplify the reference list of microhabitats to be

sampled and to keep only the ones which are the least sensitive to observer effect and the most correlated to biodiversity. However, in our study we detected widely varying degrees of effect; this indicates that observer effects related to such a simplified list should be carefully tested. The study of the correlations between microhabitat types (Regnery et al., 2013b) or the influence of tree characteristics (Vuidot et al., 2011) may also help to determine which microhabitat type(s) or tree characteristic(s) best represent the others. Our point here is clearly not to propose a systematic simplification, as previous studies on microhabitats have shown their importance in assessing sustainable forestry or specific biodiversity (Michel and Winter, 2009; Winter and Möller, 2008). However, such a solution should be considered depending on the census objectives. For example, for monitoring or biodiversity-friendly management purposes, a simplified version such as the one used in strict forest reserves in Switzerland (Tinner et al., 2012) may be enough.

4.3. Implications for the validation of microhabitats as a biodiversity indicator

Despite the strong effect we detected, it is worth noting that it was comparable to levels observed in other studies, even with experts only, notably on birds, vascular plants, and forest health (Chen et al., 2009; Ferretti et al., 2014; Pacifici et al., 2008). However, it also proves that microhabitat are not as easy to inventory as it has been recently claimed (Regnery et al., 2013a), especially when observers are not used to such protocols. Although not new for measurements in ecology, observer effects have never been quantified before for tree microhabitats, and as this research object has recently gained attention as biodiversity indicator, we assume that the present study is necessary in the validation process (Regnery et al., 2013a; Vuidot et al., 2011). In agreement with several studies, we believe that observer effects have too often been overlooked in biodiversity and other environmental assessments (Archaux et al., 2009) and should be further integrated into validation, collection and/or analysis processes, notably when ecological indicators are involved. Although observer biases may strongly influence results and their interpretation (Ahrends et al., 2011; Archaux, 2009), they only become a problem if they are systematic with respect to the effects that are being tested (Manu and Cresswell, 2007), *e.g.* if the same observers systematically observe the same modalities in an experiment. However, observer effects also induce less precise estimates in data analyses, and this may compromise the detection of certain effects (Manu and Cresswell, 2007).

In terms of indicator validation – in our case to link specialized forest biodiversity with microhabitat types – and monitoring, it is important to take into account and control for potential observer effect, for example by using a limited number of experienced observers (Vuidot et al., 2011). Other ways to limit observer effects have been proposed above and should be applied by experts, or volunteers in case of participatory monitoring, for data quality to be preserved (Ahrends et al., 2011; Allegrini et al., 2009). Although we did not demonstrate a clear difference between experienced and inexperienced observers in this study, special care should be taken for observations made by volunteers with different backgrounds in citizen monitoring. Alternatively, these indicators could be set aside until ways to reduce observer effect to more reasonable levels have been found. Such indicators could ultimately be abandoned if the levels of uncertainty linked with them are unacceptable. Finally, both researchers and managers must recognize that there is no such thing as an ideal or perfect method; but there are ways to make their results and monitoring as reliable as possible. Limiting observer effects is one that should not be overlooked.

5. Acknowledgements

We are indebted to H. Martin for his implication as an independent observer for the reference census. We are grateful to the volunteers for their cheerfulness and willingness during the test. Many thanks to: P. Anselle, D. Ballon, I. Bilger, A. Chevalier, G. Defour, L. Larrieu, A. Lassauce, B. Nusillard, M. Picard, A. Pouzerat and A. Villemey. We also thank V. Moore for strongly polishing the language. Two anonymous reviewers' comments improved the present manuscript. This research was funded by the

French Ministry in charge of Ecology (Convention Cemagref-DEB (MEEDDAT), Action GNB and the program “Biodiversité, Gestion Forestière et Politiques Publiques” (BGF), convention GNB 10-MBGD-BGF-1-CVS-092, no CHORUS 2100 214 651) and the Office National des Forêts (Convention ONF-Cemagref, Action 5, 2008).

6. References cited

Ahrends, A., Rahbek, C., Bulling, M.T., Burgess, N.D., Platts, P.J., Lovett, J.C., Kindemba, V.W., Owen, N., Sallu, A.N., Marshall, A.R., Mhoro, B.E., Fanning, E., Marchant, R., 2011. Conservation and the botanist effect. Biol. Conserv. 144, 131-140.

Allegrini, M.C., Canullo, R., Campetella, G., 2009. ICP-Forests (International Co-operative programme on assessment and monitoring of Air pollution effects on forests): Quality assurance procedure in plant diversity monitoring. J. Environ. Monit. 11, 782-787.

Archaux, F., 2009. Could we obtain better estimates of plot species richness from multiple-observer plant censuses? J. Veg. Sci. 20, 603-611.

Archaux, F., Bergès, L., Chevalier, R., 2007. Are plant censuses carried out on small quadrats more reliable than on larger ones? Plant Ecol. 188, 179-190.

Archaux, F., Camaret, S., Dupouey, J.L., Ulrich, E., Corcket, E., Bourjot, L., Brethes, A., Chevalier, R., Dobremez, J.F., Dumas, Y., Dume, G., Foret, M., Forgeard, F., Gallet, M.L., Picard, J.F., Richard, F., Savoie, J.M., Seytre, L., Timbal, J., Touffet, J., 2009. Can we reliably estimate species richness with large plots? an assessment through calibration training. Plant Ecol. 203, 303-315.

Archaux, F., Gosselin, F., Bergès, L., Chevalier, R., 2006. Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. J. Veg. Sci. 17, 299-306.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127-135.

Butt, N., Slade, E., Thompson, J., Malhi, Y., Riutta, T., 2013. Quantifying the sampling error in tree census measurements by volunteers and its effect on carbon stock estimates. Ecol. Appl. 23, 936-943.

Chen, G., Kéry, M., Zhang, J., Ma, K., 2009. Factors affecting detection probability in plant distribution studies. J. Ecol. 97, 1383-1389.

Cline, S.P., Burkman, W.G., 1989. The role of quality assurance in ecological programs, in: Bucher, J.B., Bucher-Wallin, I. (Eds.), Proceedings of the 14th International Meeting for Specialists in Air Pollution Effects on Forest Ecosystems, IUFRO P2.05, Interlaken, Switzerland, pp. 361-365.

Dawson, D.K., Efford, M.G., 2009. Bird population density estimated from acoustic signals. J. Appl. Ecol. 46, 1201-1209.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X., 2001. Analysis of aggregation, a worked example: Numbers of ticks on red grouse chicks. Parasitology 122, 563-569.

Fenton, N.J., Bergeron, Y., 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. Biol. Conserv. 141, 1389-1399.

Ferretti, M., 2013. A quality assurance framework for designing forest monitoring programs, in: Ferretti, M., Fischer, A. (Eds.), Forest monitoring. Methods for terrestrial investigation in Europe with an overview of North America and Asia, 1st ed. Elsevier, pp. 77-90.

Ferretti, M., Beuker, E., Calatayud, V., Canullo, R., Dobbertin, M., Eichhorn, J., Neumann, M., Roskams, P., Schaub, M., 2013. Data quality in field surveys. Methods and results for tree condition, phenology, growth, plant diversity and foliar injury due to ozone, in: Ferretti, M., Fischer, A. (Eds.), Forest monitoring. Methods for terrestrial investigation in Europe with an overview of North America and Asia., 1st ed. Elsevier, pp. 397-414.

Ferretti, M., Fischer, A., 2013. Forest monitoring. Methods for terrestrial investigation in Europe with an overview of North America and Asia, 1st ed. Elsevier.

Ferretti, M., Nicolas, M., Bacaro, G., Brunialti, G., Calderisi, M., Croisé, L., Frati, L., Lanier, M., Maccherini, S., Santi, E., Ulrich, E., 2014. Plot-scale modelling to detect size, extent, and correlates of changes in tree defoliation in French high forests. For. Ecol. Manag. 311, 56-69.

Gotfryd, A., Hansell, R.I.C., 1985. The impact of observer bias on multivariate analyses of vegetation structure. Oikos 45, 223-234.

Innes, J.L., 1988. Forest health surveys: problems in assessing observer objectivity. Can. J. For. Res. 18, 560-565.

Kendall, W.L., Peterjohn, B.G., Sauer, J.R., 1996. First-time observer effects in the North American Breeding Bird Survey. Auk 113, 823-829.

Koop, H., Hilgen, P., 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (Fagus sylvatica) stands at Fontainebleau (France). For. Ecol. Manag. 20, 135-150.

Larjavaara, M., Muller-Landau, H.C., 2013. Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. Meth. Ecol. Evol. 4, 793-801.

Manu, S., Cresswell, W.R.L., 2007. Addressing sampling bias in counting forest birds: A West African case study. Ostrich 78, 281-286.

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. For. Ecol. Manag. 257, 1453-1464.

Nichols, J.D., Hines, J.E., Sauer, J.R., Fallon, F.W., Fallon, J.E., Heglund, P.J., 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117, 393-408.

Pacifici, K., Simons, T.R., Pollock, K.H., 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. Auk 125, 600-607.

Pontailler, J.Y., Faille, A., Lemée, G., 1997. Storms drive successional dynamics in natural forests: a case study in Fontainebleau forest (France). For. Ecol. Manag. 98, 1-15.

R Core Team, 2012. R: A language and environment for statistical computing., in: R Foundation for Statistical Computing (Ed.), Vienna, Austria.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., Kerbiriou, C., 2013a. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Indic. 34, 221-230.

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013b. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? For. Ecol. Manag. 295, 118-125.

Riffell, S.K., Riffell, B.D., 2002. Can observer clothing color affect estimates of richness and abundance? An experiment with point counts. J. Field Ornithol. 73, 351-359.

Scott, W.A., Hallam, C.J., 2003. Assessing species misidentification rates through quality assurance of vegetation monitoring. Plant Ecol. 165, 101-115.

Strand, G.H., 1996. Detection of observer bias in ongoing forest health monitoring programmes. Can. J. For. Res. 26, 1692-1696.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19, 305-308.

Tinner, R., Streit, K., Commarmot, B., Brang, P., 2012. Stichprobeninventur in schweizerischen Naturwaldreservaten - Anleitung zu Feldaufnahmen. Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmesndorf, Eidg., p. 44.

Vales, D.J., Bunnell, F.L., 1988. Comparison of methods for estimating forest overstory cover. I. Observer effects. Can. J. For. Res. 18, 606-609.

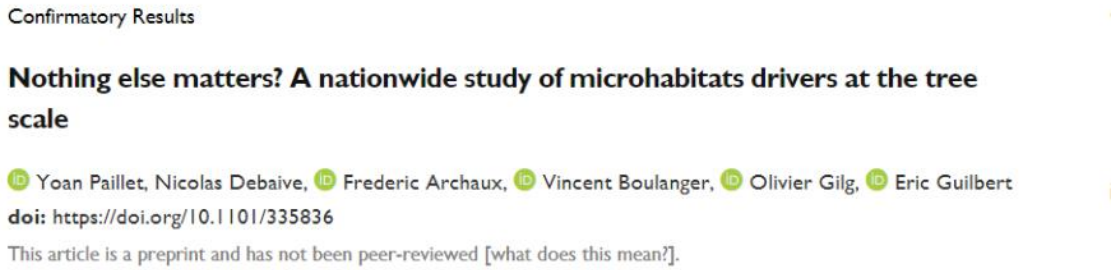
Venier, L.A., Holmes, S.B., Holborn, G.W., McIlwrick, K.A., Brown, G., 2012. Evaluation of an automated recording device for monitoring forest birds. Wildl. Soc. Bull. 36, 30-39.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats in France. Biol. Conserv. 144, 441-450.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manag. 255, 1251-1261.

Chapitre 3 - Mieux comprendre les facteurs d'influence à différentes échelles

3.1. A l'échelle de l'arbre : "Nothing else matters? A nationwide study of microhabitats drivers at the tree scale" – Paillet et al. Preprint.



Confirmatory Results

Nothing else matters? A nationwide study of microhabitats drivers at the tree scale

Yoan Paillet, Nicolas Debaive, Frederic Archaux, Vincent Boulanger, Olivier Gilg, Eric Guilbert

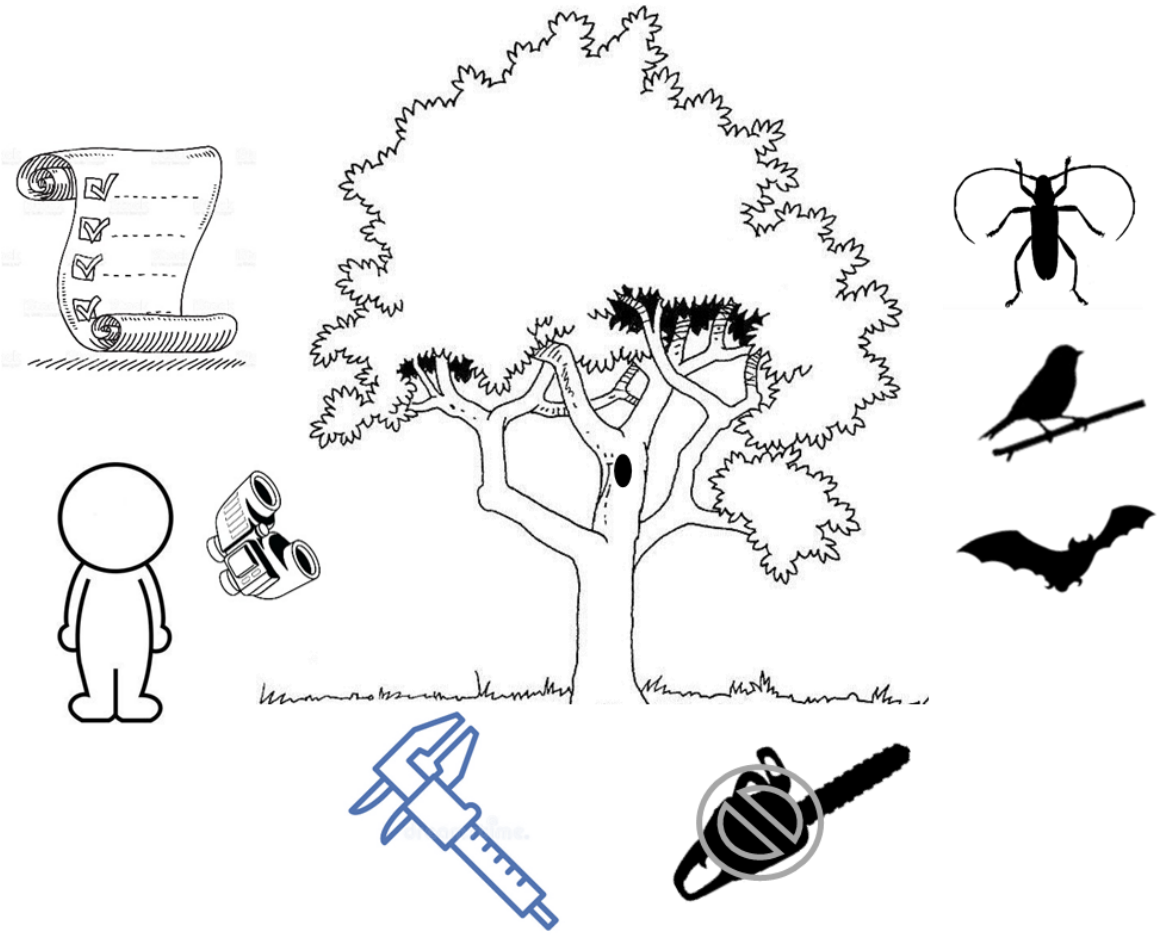
doi: https://doi.org/10.1101/335836

This article is a preprint and has not been peer-reviewed [what does this mean?].

Résumé

Gérer la structure forestière dans le but de préserver la biodiversité nécessite une bonne connaissance des éléments qui favorisent effectivement la biodiversité ainsi que des déterminants de leur dynamique. Les microhabitats des arbres (cavités, fentes, carpophores de champignons) sont des caractéristiques des arbres réputées favoriser une biodiversité spécifique, qui dépend des microhabitats pour au moins une partie de son cycle de vie. Alors que plusieurs études ont analysé les facteurs d'influence du nombre et de l'occurrence des microhabitats à l'échelle de l'arbre, elles demeurent limitées à un petit nombre d'espèces d'arbre dans un domaine biogéographique relativement restreint. Ici, nous avons utilisé une base de données nationale issue des réserves naturelles forestières françaises qui comprend plus de 22000 arbres où les microhabitats ont été inventoriés depuis 2005. Nous avons analysé les effets du diamètre de l'arbre et de la vitalité (arbres vivants vs morts) sur le nombre et l'occurrence des microhabitats, en prenant en compte des variables biogéoclimatiques et l'essence d'arbre.

Nous avons confirmé que les plus gros arbres ainsi que les arbres morts portaient plus de microhabitats que leurs équivalents plus petits ou vivants, et nous avons étendu ces résultats à plusieurs essences d'arbres dans des conditions variées. Contrairement à nos hypothèses, ces relations ne variaient pas beaucoup que ce soit en fonction de l'essence d'arbre – avec des niveaux d'accumulation avec le diamètre à peine plus élevés sur les feuillus que sur les conifères – ou du contexte biogeographique. Nous avons observé les mêmes résultats pour le nombre total de microhabitats par arbre et pour l'occurrence des microhabitats individuels. Cependant, ces relations étaient plus marquées pour les microhabitats liés à la décomposition des arbres (*e.g.* branches mortes ou trous de nourissage de pics) que pour les autres microhabitats epixyliques, comme les épiphytes (lierre, mousses et lichens). Préserver les gros arbres vivants et les chandelles d'essences diverses semble une façon adéquate et relativement universelle de favoriser les microhabitats et améliorer la capacité d'acceuil pour certaines espèces qui en dépendent. De plus, une meilleure compréhension des facteurs d'influence des microhabitats à l'échelle de l'arbre pourrait contribuer à mieux les définir comme indicateurs de biodiversité dans l'optique d'un suivi à large échelle.



Nothing else matters? A nationwide study of microhabitats drivers at the tree scale

Yoan Paillet[1,2*], Nicolas Debaive[3,] Frédéric Archaux[1], Vincent Boulanger[4], Olivier Gilg[3], Eric Guilbert[2]

[1] Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France
[2] MECADEV, UMR 7179 MNHN/CNRS, CP50, 57 rue Cuvier, 75005 Paris, France
[3] Réserves Naturelles de France, La Bourdonnerie, 2 allée Pierre Lacroute – CS 67524 – 21075 Dijon cedex
[4] Office National des Forêts, Département Recherche et Développement, Boulevard de Constance, 77300 Fontainebleau, France
*Corresponding author: yoan.paillet@irstea.fr

Abstract

Managing forest structure to preserve biodiversity requires a good knowledge of the elements that actually support biodiversity as well as the driving factors of their dynamics. Tree-related microhabitats (cavities, cracks, conks of fungi) are tree-borne features that are reputed to support specific biodiversity, linked to microhabitats for at least a part of their life cycle. While several studies have analysed the drivers of microhabitats number and occurrence at the tree scale, they remain limited to a few tree species located in relatively narrow biogeographical range. Here, we used a nationwide database of forest natural reserves comprising more than 22000 trees where microhabitats have been inventoried since 2005. We analysed the effect of tree diameter and live status (alive or dead) on microhabitat number and occurrence per tree, taking into account biogeoclimatic variables and tree genus.

We confirmed that larger trees as well as dead trees bore more microhabitats than their smaller or alive counterparts, and extended these results to a wider range of tree genus and conditions. Contrary to expectations, these relationships varied neither much with tree genus, with slightly higher accumulation levels for broadleaves than for conifers, nor with biogeographical context. We observed these results both for the total number of microhabitats per tree and for the occurrence of individual microhabitat types. However they were more marked for microhabitats linked with wood decay processes (*e.g.* dead branches or woodpecker feeding holes) than for other, epixylic, microhabitats such as epiphytes (ivy, mosses and lichens).

Promoting large living and dead trees of several tree species seems a good and quite universal way to promote microhabitats and enhance potential substrates to support specific biodiversity. In addition, a better understanding of the drivers of microhabitats at the tree scale may help to better define them as biodiversity indicators for large scale monitoring.

Keywords: Tree-related microhabitats; Diameter at breast height; Tree vitality; Biodiversity indicator.

Introduction

Small natural features are defined as structural habitat elements that have a disproportionate role for biodiversity regarding their actual size [1]. Taking them into account in biodiversity conservation appears as a new frontier in terms of science-based decision making [2]. In forests, delineating such elements is quite challenging since the number and variety of candidate structural features in a tri-dimensional environment is potentially infinite. Small natural features encompass for example large old trees [3] as well as tree-born structures. While large old trees are disappearing at the large scale [4], their importance for biodiversity remains partially unknown, not to speak of the peculiarities they are susceptible to bear (ie. cracks, cavities, epiphytes) that are also known as 'tree-related microhabitats' (hereafter 'microhabitats', [5]). Microhabitats have recently met the interests of scientists and forest managers since they can serve as a substrate for a specific part of forest biodiversity [5,6] and ultimately as forest biodiversity indicators [5,7]. Their conservation in daily forest management has hence become an issue, just like large old trees and deadwood [8,9]. However, our understanding of their dynamics and driving factors, notably at the tree scale, remains incomplete [10]. Tree diameter and live status (alive vs dead trees) have been shown as key factors for microhabitat presence and number at the tree scale [11-13]: larger trees are likely to bear more microhabitats than smaller trees, as they have experienced more damages and microhabitats-creating events (*e.g.* woodpecker excavation, storms, snowfalls); similarly, dead trees are likely to bear more microhabitats than living trees, relatively to the decomposition process and their role as habitat and food source for many microhabitat-creating species [14]. The relationships between microhabitats and tree characteristics have nevertheless been demonstrated on a limited number of tree species involving only a maximum of a few thousand observations at the tree level (*e.g.* [10-12]), and within a limited biogeographical range (see case studies in Mediterranean forests [15], the French Pyrénées [11] or in Germany [16,17]). As a consequence, the question still remains whether the observed relationships between tree characteristics and microhabitats are idiosyncratic or not. Large databases allowing such analysis at a larger scale are currently rare (but see [18]) due mainly to a lack of homogeneity in the typologies used to inventory microhabitats [5], but also to the scarcity of forest monitoring initiatives that actually inventory microhabitats. Such sources of information are crucial to better understand the potential variations of these relationships with biotic (*e.g.* tree species) or abiotic (e.g climatic) factors. Since microhabitats are on the potential biodiversity indicator list [7,16,19], it is also important to better understand the factors of influence at various scales, including the tree scale.

In this context, we benefited from a nationwide database issued of forest monitoring in nature reserves, where microhabitats have been inventoried since 2005. Based on this, we analysed the influence of individual tree diameter and living status on the number and presence of microhabitats at the tree level. We expected the number and occurrence of microhabitats per tree to increase with diameter and to be higher on dead than living trees. We assessed the influence of tree species as well as the influence of aggregated biogeoclimatic variables on these relationships, expecting that the microhabitat dynamics (or accumulation rate per tree) would be tree-species dependent and vary with abiotic context. Ultimately, the aim of this study was to provide forest managers with a better – science-based – understanding of the forest ecosystem with a special focus on microhabitats, allowing them to adapt their management to their specific context.

Materials and methods

Database structure

We worked with a nationwide database issued of the monitoring program in French forest reserves. Since 2005, a systematic permanent plot network has been gradually set-up on a voluntary basis in several forest reserves. The main aim was to provide managers with quantitative data on the fluxes of living and dead trees at the site scale, and ultimately delineate guidelines for management plans establishment. The full database currently comprises 107 reserves for a total of 8190 plots (83180

living and 19615 dead trees, snags and stumps). Forest management in the reserves varies from total abandonment (strict forest reserves) to active management aimed at preserving specific biodiversity (special forest reserves). However, no homogeneous data could be gathered at the plot level for all the reserves in the database. In addition, Vuidot et al. [12] shown that management had a limited effect on microhabitats number and occurrence at the tree level. For these two reasons, we assume that management differences do not play a significant role at the tree scale and did not take into account this source of variation in the analyses (see below).

Microhabitat	Description	Occurrence (%, n=22307)
Base Cavity	Non-woodpecker cavity located at a height < 1.3m, large enough to host small mammals	9.2
Trunk Cavity	Non-woodpecker cavity located at a height comprised between 1.3m and the first main branch	4.5
Canopy cavity	Non-woodpecker cavity located on canopy branches (unhealed)	1.0
Woodpecker cavity	Nesting cavity of a woodpecker, minimum diameter 2cm	1.4
Crack	Crack in the wood with a width >1cm and deep enough to host bat species	3.1
Woodpecker feeding hole	Feeding hole dug by a woodpecker	4.6
Rot	Presence of wood rot	3.3
Injury	Fresh injury, minimum diameter 10cm.	12.1
Conk of fungi	Conk of perennial polypore	4.0
Bark characteristic	Bark loosened affecting >50% of the surface of a given part of the tree (base, trunk, canopy)	3.1
Bryophyte (>50)	Epiphytes with a cover >50% of a given part of the tree (base, trunk, canopy)	53.5
Lichen (>50)		31.9
Ivy (>50)		7.9
Small branches (5-10cm)	Dead branches with a diameter comprised between 5 and 10cm and a length higher than 1m	28.4
Medium branches (10-30cm)	Dead branches with a diameter comprised between 10 and 30cm and a length higher than 1m	13.3
Large branches (>30cm)	Dead branches with a diameter higher than 30cm and a length higher than 1m	1.5
Crown skeleton	Noted when the sum of small, medium and large branches is higher than 10 individuals	2.3
Fork	Fork with suspected presence of organic matter or rainwater	12.8
Broken stem	Broken or dry main stem	7.1

Tableau 13 : Typology of microhabitats

Stand structure and microhabitat inventories

On each plot, forest stand structure was characterised using a combination of two sampling methods [20]. For all living trees with a diameter at breast height (DBH) higher than 30 cm, we used a fixed angle plot method to select the individuals comprised within a fixed relascopic angle of 3%. Practically, this meant that the sampling distance is proportional to the apparent DBH of a tree: for example, a tree with a DBH of 60 cm was included in the sample if it was comprised within a maximum distance of 20 m from the centre of the plot. This particular technique allows large trees to be more precisely estimated at a small scale. All other variables were measured on fixed-area plots. Within a fixed 10 m (314m2) radius around the plot centre, we measured (i) the diameter of all living trees from 7.5 to 30 cm DBH in lowlands and (ii) snags (standing dead trees with height > 1.30 m, to the exclusion of stumps below this height) with a diameter ≤ 30 cm. Within a 20 m radius (1256 m2), we recorded the diameter

of snags with a diameter > 30 cm. All trees, either alive or dead, were determined to species level whenever possible. In the following, tree species were grouped at the genus level to have sufficient representation in terms of tree numbers (namely: Ash, Beech, Chestnut, Fir, Hornbeam, Larch, Maple, Oak, Pine, Poplar and Spruce). By this, we assumed that tree genus, rather than species, did influence the relationships we studied. Undetermined tree species or genus were excluded.

All standing trees selected were visually inspected for microhabitats and the presence of microhabitat was recorded on each tree. Observers were provided with a field guide including pictures for better determination of microhabitats and detailing the criteria of inclusion in the inventories. Although probably imperfect compared with recent developments [5,21], this method has limited the potential observer effect linked with microhabitat inventories [22].

Microhabitat inventories were based on different typologies due to parallel developments and lack of harmonization since 2005. As a consequence, we selected only a part of the data in the database to be as homogeneous a possible and to avoid too much degradation of the original data by grouping microhabitat types to coarser classification grains.

	Living trees					Dead trees				
Genus	**ST**	**MT**	**LT**	**VLT**	**Total**	**ST**	**MT**	**LT**	**VLT**	**Total**
Ash	300	292	93	25	710	25	11	3	0	39
Beech	1743	3382	1811	600	7536	117	213	100	37	467
Chestnut	71	154	87	26	338	42	14	4	3	63
Fir	807	1440	1339	698	4284	126	348	155	54	683
Hornbeam	223	156	30	2	411	8	4	1	0	13
Larch	114	312	243	79	748	6	11	2	0	19
Maple	375	472	140	19	1006	21	10	3	0	34
Oak	1259	1549	1043	925	4776	79	89	38	33	239
Pine	363	783	273	33	1452	83	115	25	5	228
Poplar	66	124	50	18	258	12	11	6	2	31
Spruce	540	850	544	330	2264	87	198	70	26	381
Total	5861	9514	5653	2755	23783	606	1024	407	160	2197

Tableau 14 : Distribution of the data by genus and Diameter at Breast Height (DBH) classes: small trees (ST: 17.5 < DBH ≤ 30), medium trees (MT, 30 ≤ DBH < 47.5cm), large trees (LT, 47.5 ≤ DBH < 67.5cm) and very large trees (VLT, DBH ≥ 67.5cm). Genus in grey were excluded from the main analyses due to small occurrences among dead trees (see Supplementary Materials: Annexe 6).

Data selection and biogeoclimatic variables extraction

First, we focused on the microhabitat typology that has been used over the larger number of plots and sites (Tableau 13). This reduced the dataset to 43 sites comprising 3165 plots. Second, smallest trees (7.5≤DBH≤17.5cm) were the more abundant in the database but also the less likely to bear microhabitats. Since this might cause zero-inflation, we excluded this category from the dataset. Third, among the remaining standing dead trees and snags, some genus were poorly represented (ie. less than 100 occurrences over the whole dataset, Tableau 14: Ash, Chestnut, Hornbeam, Larch, Maple, Poplar). In order to be able to account for the tree live status in the statistical models (ie. living vs dead trees, see below), we excluded these groups to conserve only those that were sufficiently represented in the two live status categories (Tableau 14, but see also Supplementary Materials: Annexe 6, for a representation on a larger subset of living trees). The final dataset comprised 2783 plots distributed over 43 sites, for a total of 22307 trees (20312 living and 1995 dead trees).

Based on plot locations, we gathered different biogeoclimatic variables:

- Annual mean temperature (bio1) and precipitation (bio12) from the Worldclim2 database [23];
- Elevation, aspect and slope from the national digital elevation model (resolution 30m);
- Plant-bioindicated pH issued from the national forest inventory [24].

Statistical analyses

Following Zuur et al. [25], preliminary data exploration did not reveal any potential variation of the relationship between microhabitat metrics and any of the biogeoclimatic variable mentioned above, apart from elevation. This latter variable was also strongly correlated to the tree species analysed (trivially, only Beech was distributed over the whole elevation gradient while the others were elevation-dependent). To account for these strongly correlated variables, we computed a principal component analysis (PCA) including mean temperature and precipitation, elevation, slope and pH (aspect was excluded as it was quite redundant with elevation) and we kept the first two uncorrelated axes for inclusion in the models detailed below (altogether these axes represented 78% of the overall variance).

We used DBH, live status (alive vs dead) and genus (Beech, Fir, Oak, Pine and Spruce) as explanatory variables. Second and third order interactions were included as well in the models. Eigenvalues of the PCA calculated above were added as well but without interactions with other variables.

We modelled the total number of microhabitat types per tree as a response variable with generalised linear mixed models (GLMMs, library glmmTMB, [26]) with Poisson error distribution for count data and plot identity nested within site as random variable. The occurrence of each microhabitat type was modelled similarly, but with binomial error distribution for binary data. Differences of microhabitats number and occurrences between living and dead trees were tested using post-hoc multicomparison Tukey tests for a fixed mean DBH (44cm; function cld, library emmeans [27]). Dispersion diagnostics revealed underdispersed model estimations, which may cause a type II error rate inflation [28]. However, since there was no simple way to account for that in a frequentist framework, we kept with these results, bearing in mind that our results were conservative despite the large number of observations we analysed. In addition, we focused our interpretations on magnitude of the results rather than statistical significance (see *e.g.* [29]). We processed all the analyses with the R software v. 3.4.3 [30].

Results

Number of microhabitats per tree

Single parameters estimates were significant in the model (apart from PCA second axis coordinates), while second order and third order interactions were less often and less significant (Supplementary Materials, Annexe 3). All tree genus except Pine had higher microhabitat number on dead than living trees. Overall, the difference was higher for Oak and Pine (resp. 50% and 43% more on dead trees for a mean DBH, Tableau 15), than for the other genus (around 30% more on dead trees). Globally, number of microhabitats per tree increased with tree diameter both for live and dead trees. However, the accumulation of microhabitat with diameter varied with genus, with higher accumulation levels for broadleaves (Beech and Oak) than for conifers (Fir, Pine, Spruce), but also for dead compared to living trees (except for Pine; Figure 6, Supplementary Materials, Annexe 4).

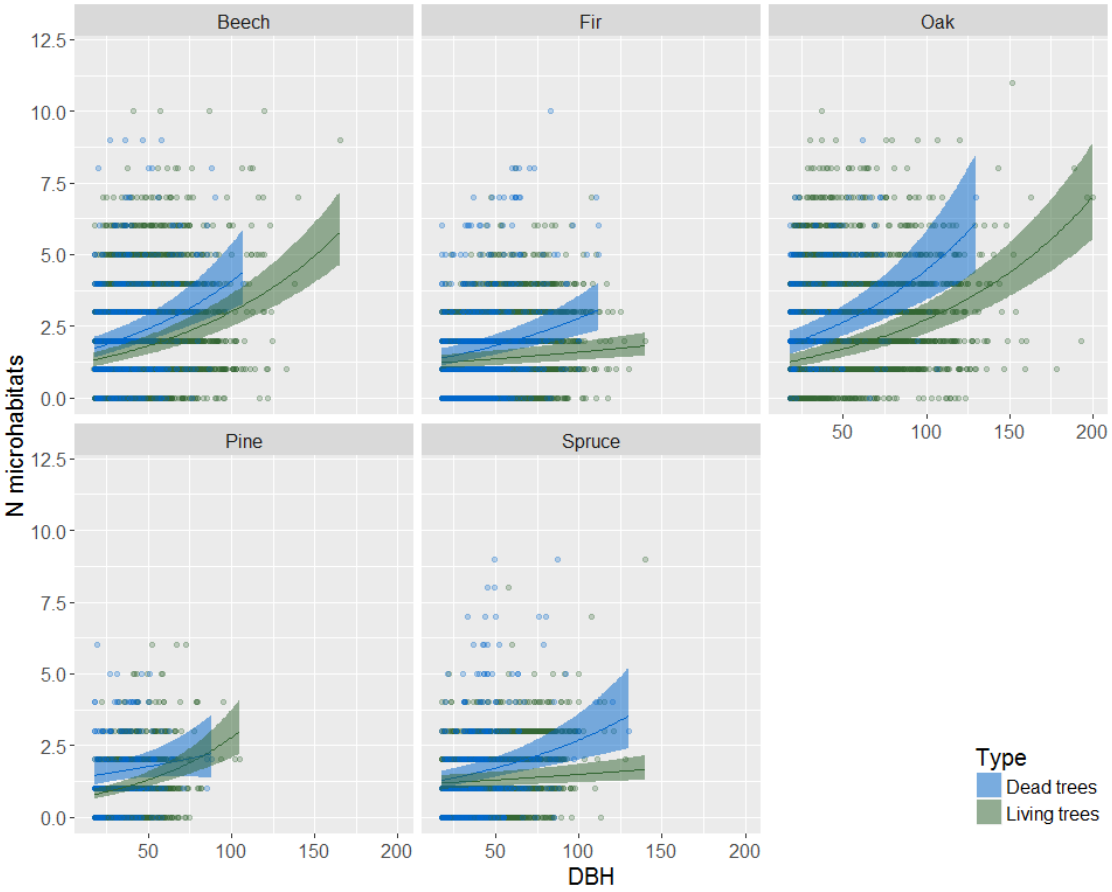


Figure 6 : Relationship between number of microhabitats (N microhabitats) per tree and Diameter at Breast Height (DBH) by species and live status (living vs dead standing trees). The line represents the estimation issued from a generalized mixed effect mode with Poisson error distribution. The ribbons represent the 95% confidence interval of the mean. Principal component analysis eigenvalues were hold constant for the representation.

Occurrence of microhabitat types per tree

Five microhabitats out of twenty showed generally higher occurrence on standing deadwood than on living trees, but not systematically for all species or for all live status: trunk cavities (broadleaves), woodpecker feeding holes, rot (broadleaves), conks of fungi (except Pine) and bark characteristics (except Pine and Spruce, Tableau 15 and Annexe 5). Conversely, injuries, dead branches whatever their size, and forks (broadleaves) showed higher occurrence on living trees. The strongest interpretable differences were observed for woodpecker cavities (*e.g.* they occurred around 300% more often on standing dead Beech, Oak and Pine, for a mean DBH = 44cm). Magnitudes for microhabitats which occurred more on living trees were smaller, *e.g.* for small branches or injuries (around 60% to 90% more on living trees, Tableau 15).

For most microhabitats, probability of occurrence increased with DBH, either for living or dead trees with the remarkable exceptions of woodpecker cavities, cracks and crown skeletons (Supplementary Materials: Annexe 5, Annexe 7). However, the magnitude of the relation varied with tree genus and live status, the increase in occurrence with DBH being higher for dead than for living trees (*e.g.* 30% more base and trunk cavities on dead Beech, 22 to 44% more woodpecker feeding holes, except on Pine). For living trees, the magnitude was generally smaller, except for occurrence of small and medium branches (*e.g.* 70% more medium dead branches on living Pine) and to a lesser extent for mosses on Beech and Fir (18% and 23% more respectively). All other magnitudes were smaller, generally below 10%. Note that in some cases, due to the very small occurrence of some microhabitats

on some tree genus (*e.g.* canopy cavities on Spruce), the estimations proved unreliable in these cases (Supplementary Materials: Annexe 5, Annexe 7).

Microhabitats	Beech	Fir	Oak	Pine	Spruce
All	-31.0*	-30.2*	-53.3*	-43.2*	-27.2*
Base cavities	-58.1	-83.3	-6.8	-227.4	52.1
Trunk cavities	-168.7*	-581.4*	-198.1*	-595*	< -1000*
Canopy cavities	34.5	-5.8	-45.2	100	< -1000
Woodp. cavities	-692.4*	-145.6	-363.5*	-380.5	-77.3
Cracks	-83.9*	-141	-978.4*	56.8	-260.5*
Woodp. feeding holes	< -1000*	< -1000*	< -1000*	< -1000*	< -1000*
Rot	-129.1*	-67.6	< -1000*	< -1000*	-853.9*
Injuries	83.7*	91.4*	79.1*	74.8*	93.0*
Conks of fungi	< -1000*	< -1000*	< -1000*	< -1000*	< -1000*
Bark characteristics	< -1000*	< -1000*	< -1000*	< -1000*	< -1000*
Moss cover >50%	27.3*	55.4*	69.1*	-249.6	-15.5
Lichen cover > 50%	83.2*	83.1*	46.6	37.6	86.1*
Ivy cover >50%	18.1	60.3	-3.3	-43.1	33.4
Small branches	90.8*	68*	94*	90.6*	60.7
Medium branches	74.3*	< -1000*	74.9*	57.5	63.3
Large branches	-90.8	-129.3	68.7	-223.4	100.0
Crown skeleton	< -1000*	-355.3	< -1000*	-659.4*	< -1000*
Forks	97.4*	83.6*	67.4	88.8	80.5*
Broken stem	-17.6	-7.3	1.3	29.5	3.4

*Tableau 15 : Percentage of difference between living and dead trees for a mean Diameter at Breast Height (DBH = 44cm) calculated as [(Microhabitat living trees – Microhabitats dead trees) / Microhabitat living trees]. * indicate significant differences based on post-hoc Tukey tests for a mean DBH. Differences lower than -1000% correspond to cases where a given microhabitat was almost absent from living trees. In these cases, the percentage was considered uninterpretable (although significant).*

Discussion

Numerous recent studies in various contexts showed that the number of microhabitats per tree, as well as the occurrence of some types increase with tree diameter [10,13,15] and showed higher levels on dead than living trees [11,12] . Our nationwide study based on a large tree database confirmed these relationships and extend them to a larger range of tree species in various biogeographical conditions than before. Indeed, our results concerned at least five tree genus (eleven if we take only living trees into account, Supplementary Materials: Annexe 6).

Dead trees bear more microhabitats than living trees

Standing dead trees contribute significantly to the supply of microhabitats, as they overall bore 30 to 50% more microhabitats than their living counterparts in our dataset. Dead trees could even bear a lot more microhabitats than living trees when individual types are analysed (*e.g.* woodpecker feeding holes or bark characteristics). Previous studies comparing microhabitat number between living and dead trees almost all found higher microhabitats numbers on dead trees (see [17]). However, this difference varied across studies, from 1.2x more microhabitats in Mediterranean forest [15], 2x more

in five forests in France [12], to 4x more on habitat trees in south-western Germany [31]. Our results ranged from 1.3x to 1.5x more microhabitats on dead than living trees, which is of a slightly lower order of magnitude than what was observed before, but on a larger geographical gradient. Once dead, standing trees are affected by decomposition processes that initiate and develop microhabitats [14,32,33]. Such trees could also constitute privileged foraging grounds for a number of species [5,7,19], including for example woodpeckers [33,34]. In particular, insect larvae or ants that live below the bark of more or less recently dead trees constitute a non-negligible part of some birds' diet [7,35,36]. As living trees also bear microhabitats, it seems logical that many of them persist when the tree dies and continue to evolve, or even condition the presence of other microhabitats linked with the decay process [14]. Injuries caused by logging, branch break or treefall could slowly rot and evolve in decayed cavities [5,32]. These successions likely explain why these microhabitats are more numerous on dead trees. The only exception to this global pattern concerned epiphytes and forks with accumulated organic matter, that tend to be more numerous on living trees. Ivy, mosses and lichen are likely to benefit from bark characteristics and conditions (*e.g.* pH, [37]) likely to occur only on living tree. In addition, epiphytes require a relatively stable substrate to grow or anchor, especially when they grow slowly like some species of mosses or lichens [38]. Such property is lost when the tree dies as the bark loosen and falls more rapidly than on living trees, which could cause epiphytic community replacement as well as lower levels of detection due to the absence of individuals. In a nutshell, decay processes linked to the tree death makes a clear difference between microhabitats that are linked to it (*i.e.* saproxylic microhabitats, sensu [5]) and those that are not – or less – linked to those phenomena (*i.e.* epixylic microhabitats).

Number and occurrence of microhabitats increase with tree diameter

We confirmed that microhabitat number and occurrence increase with tree diameter but, contrary to expectations, tree genus – as well as abiotic factors – had a limited effect on this relationship, with slightly higher microhabitat accumulation levels on broadleaves than conifers ([10-12], but see [13]). At the individual microhabitat level, almost all types showed the same trend, but also with considerable variations in terms of magnitude. Larger (living) trees have a generally longer lifespan than smaller ones, and are consequently more prone to damages due to meteorological events (storms, snowfall), natural hazards (rockfalls) or attacks and use by different tree- and wood-dependent species (woodpeckers, beetles, fungi, *e.g.* [12,39]). Depending on the studies, for a comparable increase in tree diameter (from 50 to 100cm), number of tree microhabitats was roughly multiplied by two in several studies [12,16,17], but can be multiplied by four [31] up to five [11] in certain cases. Our results showed magnitudes below the lower end of this range (the multiplication coefficient ranged from 1.2 to 1.4). This is probably linked to the fact that the large trees in our dataset may be younger that those in the other studies, especially compared to studies located in near-natural or long-abandoned forests [11,12]. At the individual microhabitat scale, dead branches were more prone to occur on large trees than smaller trees, which seems quite obvious but has rarely been quantified before: larger trees have more, but also larger, branches likely to die from competition with neighbours, especially broadleaves [40]. Indeed, Oak and Beech were the tree genus that showed higher large dead branches accumulation rates in our analyses, while conifers showed almost no large dead branches. Cavity bird and bats are reputed to choose preferentially larger trees to nest or roost [41,42], since larger wood width around the cavity provides buffered and more stable conditions [43]. However, this relationship was not the best shown in our results, since the accumulation rate of woodpecker cavities with tree diameter was very slow. This absence of relationship between tree diameter and woodpecker cavities seems hard to prove in the context of temperate European forests (see [12] at the tree scale, or [6] at the stand scale) and probably require more targeted examination [33,44]. This could also be linked to non-linear dynamics [10] of this particular microhabitat (some cavities in living trees can close back when they are not used anymore) but also for other microhabitats with specific phenology like conks of fungi [45]. The number and occurrence of microhabitats also

increased with diameter of standing dead trees, sometimes at a higher rate than for living trees. In this case, the longer persistence of large dead trees compared to smaller ones [46,47] may combine the effects of increased hazard and damage risks with the decay processes described above. This probably explains the higher accumulation levels we observed in many cases, especially for saproxylic microhabitats (*e.g.* rot, feeding holes, trunk cavities). Once again, the only exception to this rule was epiphytes: their probability of occurrence tended to increase with tree diameter but in a very noisy and unclear way, both for living and for dead trees. For such epiphytic organisms, larger scale processes and biogeoclimatic (*e.g.* soil fertility, precipitation) context is probably more important than local tree characteristics [48,49].

Limitations and research perspectives

We showed a limited effect of biogeoclimatic variables on the relationship between microhabitats, tree diameter and living status. However, the way we controlled for them in the models remains rather imperfect. Some specific interactions may exist, especially in the case of epiphytes [49], but could not be detected by our approach with aggregated variables. In addition, it was rather difficult to disentangle the effects of tree genus with that of biogeoclimatic variables, since distribution range of most tree species we analysed is linked to a climatic niche, apart from Beech and more marginally for Pine that occur over larger gradients. Still, the fact that we did not highlight any clear interaction with biogeoclimatic variables during exploratory analyses tend to confirm that the relations we observed are valid for a wide range of species. However, further analyses are required to assess the effects of biogeoclimatic variables on microhabitat patterns for the species with a large ecological amplitude (especially Beech species, that occur over temperate and Mediterranean Europe and beyond).

Our data is issued from nature reserves with a potentially larger anthropogenic gradient than managed forests. Some of these reserves have not been harvested for several decades and exhibit characteristics of overmature forests (see *e.g.* [22], who analysed some of the reserves included in this paper), but their overall structure reflects a relatively recent management abandonment – if any – probably marked by previous intensive harvesting and use over the past centuries characteristic of western European forests [50]. This is testified by the relatively rare occurrence of dead standing trees, in particular those with a large diameter, in the dataset we analysed: standing dead trees represented a mere 10% of the total dataset while very large individuals (DBH > 67.5cm) only 1% (Tableau 14). As a consequence, despite the fact that we worked on an extended management gradient including unmanaged strict reserves, we still lack a part of the elements characteristic of old-growth and overmature forests, especially large dead trees [20,51], which cause our relationships to be truncated and imprecise for the larger diameter categories. Further research on the last remnant of old-growth primeval forests in Europe [52] is thus needed to bridge this gap and better understand microhabitats dynamics over a whole life of a tree.

Compared to recent developments [5,21], the typology we used (Tableau 13) appears rather coarse and imprecise. But, on the one hand, it allowed us to have a sufficient number of occurrences in each types to analyse the combined effects of diameter and species for almost all microhabitat types in the typology. On the other hand, it is also likely that we were not able to confirm some effects mentioned in the literature due to imprecise distinctions between types, for example different woodpecker cavity types. The current approach should then be viewed as a compromise between sufficient occurrence of each microhabitat type in the dataset and specificity of the typology. Current developments mentioned above [5] will certainly help to homogenize data in a near future and to build larger shared databases on common and comparable bases.

Finally, our models assumed – unrealistically – microhabitat number to increase exponentially with diameter. Recent studies [17], as well as ecological theory (*e.g.* species-area relationship), tend to rather show a saturated (*e.g.* logarithmic or sigmoid) relationship between microhabitats and diameter. Models allowing for different link functions – probably within a Bayesian framework – remain to be tested to see whether they perform better than the current ones used (see *e.g.* [10]).

Implications for forest management and biodiversity conservation

Among small natural features, large and old trees are considered a keystone in forest and agro-pastoral landscapes because of their disproportionate importance for biodiversity relatively to their size [3]. This functional role for biodiversity seems further enhanced by the 'smaller' natural features – microhabitats – they bear. In this large-scale analysis, we confirmed and extended some of the results already observed locally: most microhabitats occur preferentially on living large trees and even more on dead ones. This relationship seems true for several tree species included in this analysis, and across a large gradient of ecological conditions, with minor differences in terms of accumulation rates. As a consequence, conserving and promoting large trees in daily forest management is likely to enhance the structural heterogeneity at the stand scale [20,53], including a variety of tree-borne microhabitats, that could further help to better conserve specific forest biodiversity [5,54]. Despite the fact that the diameter effect seems consistent across different conditions, promoting a variety of large trees of various species may further increase the effect on biodiversity [19], since the succession dynamics of microhabitats as well as their formation speed may vary with tree species [10,12]. Successional patterns and long-term dynamics or microhabitats remains largely unknown [10], long term monitoring at the tree and stand scales are still needed to better understand their dynamics and the underlying processes at play [5]. Ultimately, such knowledge will feed recommendations to managers to better preserve biodiversity on solid scientific grounds.

Acknowledgements

We are in debt to the reserve managers who feed the database and made this study possible. Without their commitment and implication in their daily management, such results would not have been achievable. We thank C. Bennemann for her work on GIS data extraction and R. Andrade for his invaluable help with ggplot issues.

References cited

1. Hunter ML, Acuña V, Bauer DM, Bell KP, Calhoun AJK, et al. (2017) Conserving small natural features with large ecological roles: A synthetic overview. Biological Conservation 211: 88-95.

2. Bauer DM, Bell KP, Nelson EJ, Calhoun AJK (2017) Managing small natural features: A synthesis of economic issues and emergent opportunities. Biological Conservation 211: 80-87.

3. Lindenmayer DB (2017) Conserving large old trees as small natural features. Biological Conservation 211: 51-59.

4. Lindenmayer DB, Laurance WF, Franklin JF (2012) Global decline in large old trees. Science 335: 1305-1306.

5. Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, et al. (2018) Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. Ecological Indicators 84: 194-207.

6. Paillet Y, Archaux F, Boulanger V, Debaive N, Fuhr M, et al. (2017) Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and Management 389: 176-186.

7. Regnery B, Couvet D, Kubarek L, Julien JF, Kerbiriou C (2013) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecological Indicators 34: 221-230.

8. Bütler R, Lachat T, Larrieu L, Paillet Y (2013) Habitat trees: key elements for forest biodiversity. In: Kraus D, Krumm F, editors. Integrative approaches as an opportunity fir the conservation of forest biodiversity. Freiburg, DEU: European Forest Institute. pp. 84-91.

9. Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge, UK: University Press.

10. Courbaud B, Pupin C, Letort A, Cabanettes A, Larrieu L, et al. (2017) Modelling the probability of microhabitat formation on trees using cross-sectional data. Methods in Ecology and Evolution 8: 1347-1359.

11. Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Canadian Journal of Forest Research 42: 1433-1445.

12. Vuidot A, Paillet Y, Archaux F, Gosselin F (2011) Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144: 441-450.

13. Winter S, Höfler J, Michel AK, Böck A, Ankerst DP (2015) Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. European Journal of Forest Research 134: 335-347.

14. Siitonen J (2012) Microhabitats. In: Stokland JN, Siitonen J, Jonsson BG, editors. Biodiversity in dead wood. New York, USA: Cambridge University Press. pp. 150-182.

15. Regnery B, Paillet Y, Couvet D, Kerbiriou C (2013) Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? Forest Ecology and Management 295: 118-125.

16. Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255: 1251-1261.

17. Großmann J, Schultze J, Bauhus J, Pyttel P (2018) Predictors of Microhabitat Frequency and Diversity in Mixed Mountain Forests in South-Western Germany. Forests 9: 104.

18. Kraus D, Schuck A, Bebi P, Blaschke M, Bütler R, et al. (2017) Spatially explicit database of tree related microhabitats (TreMs). Version 1.2. ed. GBIF.org: Integrate+ project, Institut National de la Recherche Agronomique (INRA).

19. Paillet Y, Archaux F, du Puy S, Boulanger V, Debaive N, et al. (submitted) The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles. Journal of Applied Ecology.

20. Paillet Y, Pernot C, Boulanger V, Debaive N, Fuhr M, et al. (2015) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. Forest Ecology and Management 346: 51-64.

21. Kraus D, Bütler R, Krumm F, Lachat T, Larrieu L, et al. (2016) Catalogue of tree microhabitats – Reference field list. Freiburg, Germany: Integrate+ Technical Paper, European Forest Insitute.

22. Paillet Y, Coutadeur P, Vuidot A, Archaux F, Gosselin F (2015) Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. Ecological Indicators 49: 14-23.

23. Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302-4315.

24. Gégout J-C Validation des bio-indicateurs floristiques pour une surveillance de l'état nutritionnel des sols forestiers français à partir des données de l'Inventaire forestier national - Rapport final,. Convention ADEME/IFN/ENGREF n° 0562C0029, 2008,. 48 p.

25. Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14.

26. Magnusson A, Skaug HJ, Nielsen A, Berg CW, Kristensen K, et al. (2017) glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R package version 0.1.3. ed.

27. Lenth R (2018) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.1. ed.

28. Sellers KF, Morris DS (2017) Underdispersion models: Models that are "under the radar". Communications in Statistics - Theory and Methods 46: 12075-12086.

29. Barbier S, Chevalier R, Loussot P, Bergès L, Gosselin F (2009) Improving biodiversity indicators of sustainable forest management: Tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. Forest Ecology and Management 258: S176-S186.

30. R Core Team (2017) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

31. Johann F, Schaich H (2016) Land ownership affects diversity and abundance of tree microhabitats in deciduous temperate forests. Forest Ecology and Management 380: 70-81.

32. Gouix N, Brustel H (2012) Emergence trap, a new method to survey Limoniscus violaceus (Coleoptera: Elateridae) from hollow trees. Biodiversity and Conservation 21: 421-436.

33. Cockle KL, Martin K, Wesołowski T (2011) Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9: 377-382.

34. Jackson JA, Jackson BJS (2004) Ecological relationships between fungi and woodpecker cavity sites. Condor 106: 37-49.

35. Zarnowitz JE, Manuwal DA (1985) The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management 49: 255-263.

36. Laiolo P, Rolando A, Valsania V (2004) Responses of birds to the natural re-establishment of wilderness in montane beechwoods of North-western Italy. Acta Oecologica 25: 129-136.

37. Mežaka A, Brumelis G, Piterans A (2012) Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. Biodiversity and Conservation 21: 3221-3241.

38. Ódor P, Király I, Tinya F, Bortignon F, Nascimbene J (2014) Reprint of: Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. Forest Ecology and Management 321: 42-51.

39. Bobiec A (2002) Living stands and dead wood in the Białowieża forest: Suggestions for restoration management. Forest Ecology and Management 165: 125-140.

40. Bouget C, Brin A, Brustel H (2011) Exploring the " last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management 261: 211-220.

41. Tillon L, Bresso K, Aulagnier S (2016) Tree selection by roosting bats in a European temperate lowland sub-Atlantic forest. Mammalia 80: 271-279.

42. Remm J, Lõhmus A (2011) Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. Forest Ecology and Management 262: 579-585.

43. Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA (2014) Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20: 495-503.

44. Edworthy AB, Martin K (2013) Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. Journal of Wildlife Management 77: 770-776.

45. Halme P, Kotiaho JS (2012) The importance of timing and number of surveys in fungal biodiversity research. Biodiversity and Conservation 21: 205-219.

46. Bobiec A, Gutowski JM, Zub K, Pawlaczyk P, Laudenslayer WF (2005) The afterlife of the tree. Warszawa-Hajnowka: WWF Poland.

47. Aakala T, Kuuluvainen T, Gauthier S, De Grandpré L (2008) Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255: 410-420.

48. Tukiainen H, Bailey JJ, Field R, Kangas K, Hjort J (2017) Combining geodiversity with climate and topography to account for threatened species richness. Conservation Biology 31: 364-375.

49. Ding Y, Liu G, Zang R, Zhang J, Lu X, et al. (2016) Distribution of vascular epiphytes along a tropical elevational gradient: Disentangling abiotic and biotic determinants. Scientific Reports 6.

50. Parviainen J (2005) Virgin and natural forests in the temperate zone of Europe. Forest Snow and Landscape Research 79: 9-18.

51. Christensen M, Hahn K, Mountford EP, Odor P, Standovar T, et al. (2005) Dead wood in European beech (Fagus sylvatica) forest reserves. Forest Ecology and Management 210: 267-282.

52. Commarmot B, Brändli U-B, Hamor F, Lavnyy V (2013) Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure: Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf; Ukrainian National Forestry University, L'viv; Carpathian Biosphere Reserve, Rakhiv. 69 p.

53. Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. Forest Ecology and Management 258: 525-537.

54. Gossner MM, Getzin S, Lange M, Pašalić E, Türke M, et al. (2013) The importance of heterogeneity revisited from a multiscale and multitaxa approach. Biological Conservation 166: 212-220.

3.2. A l'échelle de la parcelle forestière : "Snags and large trees drive higher tree microhabitat densities in strict forest reserves" – Paillet et al. For. Ecol. Man. (2017).

Forest Ecology and Management 389 (2017) 176–186

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Snags and large trees drive higher tree microhabitat densities in strict forest reserves

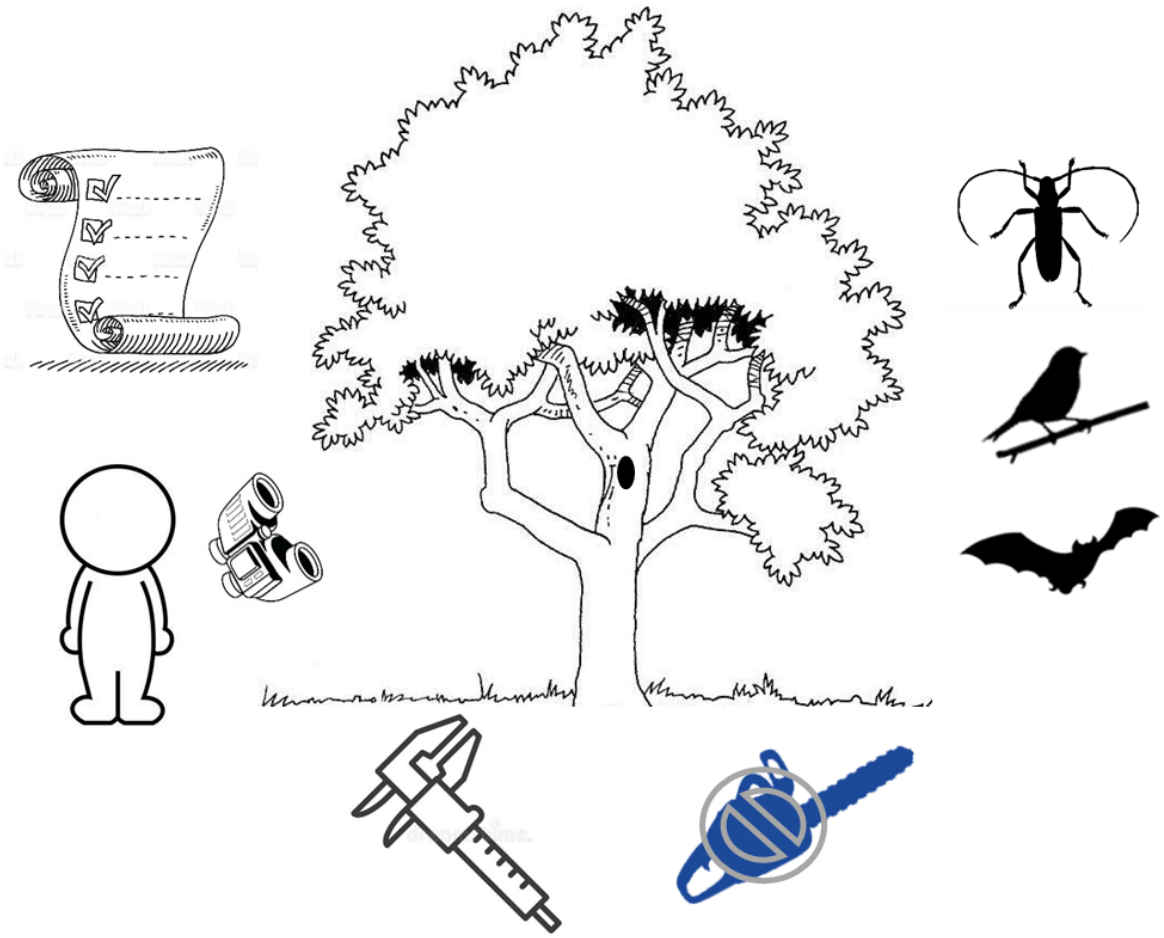
Yoan Paillet [a,b,*], Frédéric Archaux [a], Vincent Boulanger [c], Nicolas Debaive [c,d], Marc Fuhr [e], Olivier Gilg [d], Frédéric Gosselin [a], Eric Guilbert [b]

Résumé

Les microhabitats des arbres (cavités, carpophores de champignons, caractéristiques de l'écorce) jouent un rôle important à la fois pour des espèces rares et spécialisées ; leur préservation doit donc être un objectif des mesures en faveur de la biodiversité forestière. Cependant, en comparaison avec d'autres caractéristiques des vieilles forêts comme le bois mort ou les gros arbres, les microhabitats n'ont été étudiés que relativement récemment et les connaissances scientifiques les concernant restent assez limitées. Ainsi, la définition d'objectifs de densités de microhabitats dans les forêts exploitées est principalement basée sur de l'expertise plutôt que sur des données empiriques quantitatives.

Nous avons comparé les densités d'arbres porteurs de microhabitats entre des forêts exploitées pour la production de bois et des réserves forestières strictes, où l'exploitation a été abandonnée. Nous avons travaillé sur 17 massifs en France (222 placettes) situées en plaine et en montagne. Nous avons montré que les densités de microhabitats sont généralement plus fortes dans les réserves que dans les forêts exploitées, et que cette différence est principalement liée à la présence d'arbres morts debouts et de gros arbres vivants. Quoique rares, les arbres morts debouts contribuent de manière disproportionnée à la différence observée alors que les gros arbres vivants jouent un rôle significatif mais moins important. De plus, contrairement aux résultats obtenus pour d'autres caractéristiques des vieilles forêts (comme les volumes de bois mort), la différence entre forêts exploitées et réserves intégrales était plus grande en montagne qu'en plaine. Pour les microhabitats individuels, cinq sur onze en montagne et seulement un en plaine (les cavités de pics) étaient significativement plus nombreuses en réserve intégrale. Au final, la densité totale ainsi que celle de certains types de microhabitats, comme les cavités ou les caractéristiques de l'écorce, augmentait avec la date de la dernière coupe. Cette augmentation était principalement due aux arbres morts porteurs de microhabitats. Par rapport aux études précédentes dans des contextes comparables, les densités que nous avons estimées étaient généralement plus fortes ; cependant, ces comparaisons étaient possibles uniquement pour les types de microhabitats les mieux documentés.

Nos résultats confirment que l'abandon d'exploitation favorise l'abondance et la diversité des microhabitats. Cependant, leur dynamique reste peu connue et seul un suivi sur le long terme devrait permettre de comprendre les mécanismes de recrutement sous-jacents. Dans le même temps, nous résultats peuvent inspirer les gestionnaires forestiers dans leur application quotidienne de pratiques en faveur de la biodiversité.



Snags and large trees drive higher tree microhabitat densities in strict forest reserves

Yoan Paillet[1,2*], Frédéric Archaux[1], Vincent Boulanger[3], Nicolas Debaive[3,4], Marc Fuhr[5], Olivier Gilg[4], Frédéric Gosselin[1], Eric Guilbert[2]

[1] Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France
[2] MECADEV, UMR 7179 MNHN/CNRS, CP50, 57 rue Cuvier, 75005 Paris, France
[3] Office National des Forêts, Département Recherche et Développement, Boulevard de Constance, 77300 Fontainebleau, France
[4] Réserves Naturelles de France, CS 67524, 21075 Dijon cedex, France
[5] Irstea, UR EMGR, 2 rue de la Papeterie, BP 76 - 38402 St-Martin-d'Hères cedex, France
*Corresponding author: yoan.paillet@irstea.fr

Highlights

- We compared microhabitat densities between managed and strict forest reserves
- Microhabitat densities were higher in strictly protected than in managed forests
- Snags and large trees drove this difference
- The density of most microhabitat types increased with time since last harvesting
- This study may inspire biodiversity-friendly forest management methods

Abstract

Tree microhabitats (cavities, conks of fungi, bark features) play an important role for both rare and specialized species biodiversity; their preservation should therefore be targeted by biodiversity-friendly forest practices. However, when compared to other old-growth characteristics like deadwood or large trees, tree microhabitats have only recently been studied so related scientific knowledge is still relatively limited. Defining target values for microhabitat densities in managed forests is mostly based on expert knowledge rather than quantitative empirical data.

We compared the densities of microhabitat-bearing trees between managed forests, where wood is still harvested, and strictly protected forest reserves, where harvesting has been abandoned, in 17 French forests (222 plots) located in both lowlands and mountain regions. We found that microhabitat densities are generally higher in strict forest reserves than in managed forests and that this difference is mainly driven by standing dead and large living trees. Though scarce, standing dead trees over-contribute to the difference observed while large trees played a lesser but significant role. In addition, contrary to results obtained for other old-growth characteristics (such as deadwood volumes), the difference between managed and strict forest reserves was higher in mountain than in lowland forests. For individual microhabitats, five out of eleven microhabitats in mountains and only one in lowland (woodpecker cavities) were significantly more numerous in strict forest reserves than in managed forests. Finally, total microhabitat density and density of specific microhabitats such as cavities and bark features increased with time since the last harvest. This increase was also mainly supported by standing dead microhabitat-bearing trees. Compared to previous studies in comparable contexts, the densities we estimated were generally higher; however, such comparisons could only be made for the most documented microhabitat types.

Our results support the idea that management abandonment favours the abundance and diversity of microhabitats. However, microhabitat dynamics remain poorly known and only long-term monitoring will help understand underlying mechanisms of recruitment. In the meantime, our results may inspire forest managers in their application of daily biodiversity-friendly practices

Keywords: standing deadwood; large trees; time since abandonment; strict forest reserves; cavities.

Introduction

The pressure on forest ecosystems to provide goods and services, such as wood, is increasing worldwide (Millenium Ecosystem Assessment, 2005) while the surface area concerned by retention measures (*i.e.* set-aside areas) is likely to be too small to sustain forest biodiversity efficiently (Parviainen *et al.*, 2000). Preserving biodiversity in managed forests is thus a challenge, and numerous methods for implementing biodiversity-friendly forest management have been documented. Among other methods, several ones aim to promote the presence of structural elements known, or assumed, to be important for biodiversity but which are usually rare in managed forests. Such structural features include lying and standing deadwood (Christensen *et al.*, 2005; Lombardi *et al.*, 2012), habitat trees (Bütler *et al.*, 2013; Bouget *et al.*, 2014a) or more generally structural legacies issued of natural disturbances and structural heterogeneity (Franklin *et al.*, 2002; Zellweger *et al.*, 2013). Various approaches comprise silviculture for old-growth attributes (Bauhus *et al.*, 2009), integrative approaches (Bollmann and Braunisch, 2013; Kraus and Krumm, 2013), management for naturalness (Winter, 2012), retention forestry (Drapeau *et al.*, 2009; Gustafsson *et al.*, 2013) but they all share the same objective. Among the structural attributes targeted by these types of management, tree microhabitats (hereafter "microhabitats") are typically cited but most of the time overlooked due to the absence of a consensual definition or a lack of knowledge; this situation persists despite a recent gain in interest and a convergence towards standardization of census procedures (Vuidot *et al.*, 2011; Larrieu *et al.*, 2014b; Winter *et al.*, 2015). By "tree microhabitats", we mean peculiarities that are not borne by all trees including cavities, cracks, conks of fungi or bark features, and that potentially provide a necessary substratum for certain taxa during at least a part of their life cycle (Winter and Möller, 2008; Vuidot *et al.*, 2011; Siitonen, 2012; Larrieu *et al.*, 2014b).

The most often studied microhabitats to date are cavities, both excavated and decayed, for which a worldwide review has recently been published (Remm and Lõhmus, 2011). The authors point out the lack of publications in Western Europe. In France, recent studies are rare and restricted to specific forest ecosystems like mountain beech-fir forests (Larrieu and Cabanettes, 2012; Larrieu *et al.*, 2012; Larrieu *et al.*, 2014a) and Mediterranean forests (Regnery *et al.*, 2013). This review also underlines that nationwide assessments of the main microhabitat types are still lacking, or are poorly implemented, in national forest inventories (see *e.g.* Tinner *et al.*, 2012 for Switzerland; and Gao *et al.*, 2015 for a broader scope).

As a result, management recommendations concerning microhabitats and habitat trees have been largely based on intrinsic expert knowledge and clearly lack established scientific guidelines for close-to-nature forest management. For example, deciding which habitat trees to conserve for supporting forest biodiversity in managed forests may rely on the presence of certain microhabitats (Bütler *et al.*, 2013). Yet, little is known about their occurrence in forests. To fill this gap in knowledge, we need reference values covering a large spectrum of microhabitat types and biogeographical regions as well as various management situations. Such references for old-growth attributes like deadwood and large trees have recently been published for France (*e.g.* Bouget *et al.*, 2014b; Paillet *et al.*, 2015b), but data on microhabitats are less common (Larrieu *et al.*, 2014b). Values based on measurements taken in forests that have remained unmanaged, *i.e.* unharvested and without any forestry operations for a certain amount of time and that are under natural disturbance dynamics since last harvesting, may help forest managers define target values and prioritize actions. The respective roles of living and dead standing trees as sources of microhabitats at the stand level are not quantified, despite clues indicating that snags and large trees generally bear more microhabitats (*e.g.* Vuidot *et al.*, 2011). In addition, the effects of forest management abandonment on microhabitat densities may vary with context and should account for biogeographical parameters, in particular when lowland and mountain forests are compared.

We analysed the response of several microhabitat density indices to management abandonment by comparing seventeen French forests located in lowland and mountain regions containing strict forest

reserves with adjacent managed forests. We also analysed the effect of time since last harvesting on the same indices. We hypothesized that:

(i) as for other old growth attributes, the total microhabitat density should be higher in strict reserves than in managed forests;
(ii) higher densities in strict forest reserves should be primarily attributed to snags and large trees, in spite of their modest contribution to the overall microhabitat density;
(iii) the density of individual microhabitat types should differ between managed forests and strict reserves, some types being more present in managed areas (*e.g.* bark loss), and others being more present in abandoned areas (*e.g.* woodpecker cavities);
(iv) the total and individual microhabitat densities associated with strict forest reserves should increase with time since the last harvesting; and conversely, densities for microhabitats dependent on managed forests should decrease with time since the last harvesting.

Ultimately, our aim was to provide forest practitioners with values for biodiversity-friendly management and to document the dynamics of different microhabitat types with respect to management abandonment.

Materials and methods

Study sites

We compared seventeen strict forest reserves distributed across France with adjacent managed forests under the same site conditions (the sampling design is detailed in Paillet *et al.*, 2015b, and only the main points are reminded here). In a nutshell, management types roughly correspond to harvesting recommendations in French managed forest that vary locally but could be summarised as follows: tree selection and felling occur generally every 5-10 years in the lowlands, and every 10-20 years in the mountains (see below). We restricted our study to mixed lowland oak-beech-hornbeam forests (*Quercus robur* L. and *Q. petraea* (Mattus.) Liebl., *Fagus sylvatica* L. and *Carpinus betulus* L., elevation ≤ 800m) and mountain beech-fir-spruce forests (*Fagus sylvatica* L., *Abies alba* Mill. and *Picea abies* (L.) Karst., elevation > 800m).

At each of the seventeen study sites, sampling locations were randomly pre-selected on a regular 100x100m grid, then plots were selected according to site conditions observed in the field. Edaphic conditions (soil texture, depth, hydromorphy and reaction to HCl) and topography (elevation, aspect and slope) were checked in the field so that each plot within the forest reserve had its paired equivalent outside the reserve. The managed plots were selected within 5km of the forest reserve boundaries and in stands composed exclusively of native tree species of the same forest type (oak-beech-hornbeam in lowlands, beech-fir-spruce in mountains). The majority of the plots were located in mature forests (see Paillet *et al.*, 2015b) but, for the present study, plots without trees with a Diameter at Breast Height (DBH) higher than 30 cm were excluded from the analysis (which reduces the sample size compared to Paillet *et al.*, 2015b). Due to field constraints and posterior plot selection, the final sample comprised a total of 222 plots but was not fully balanced (Tableau 16).

For 187 plots, the time since last harvesting was recorded from management plans or wood sales data. Stand age was generally unavailable. The mean time since last harvesting for the strict forest reserves was 48 years (46 +/- SD 42 years in lowlands, and 50 +/- SD 38 years in mountains) and for managed forests, 9 years (7 +/- SD 5 years in lowlands and 12 +/- SD 10 years in mountains). Twenty-five plots in the strict reserves had experienced harvesting during the last 20 years before designation, while five plots in managed forests had not been harvested for more than 20 years.

Silvicultural treatments were also recorded even though they were strongly biased by elevation: 78% of the uneven-aged forests (continuous cover) were located in mountain beech-fir-spruce forests whereas all the even-aged high forests (selective cutting followed by clearcutting and natural

regeneration) were located in lowland beech-oak dominated forests. No other type of management (*e.g.* grazing) occurred in our plots. Further information on past harvesting operations either in protected or unprotected forests were very scarce and heterogeneous. As a consequence, we did not address silvicultural treatments or past harvesting intensity in our analyses (for more information on past management, see discussion in Paillet *et al.*, 2015b).

	Forest sites	n plots		Time since last harvesting (years +/-SD)		Average elevation	SFR surface (ha)
		MAN	SFR	MAN	SFR		
Lowlands	Auberive	12	12	7.3 (5.8)	24.6 (12.4)	455	232
	Bois du Parc	4	1	NA	39 (NA)	183	45
	Chizé	10	10	8.0 (3.4)	21.3 (6.6)	80	2579
	Citeaux	6	6	9.8 (3.9)	42.5 (7.4)	232	47
	Combe-Lavaux	4	4	3.3 (3.3)	37.5 (0.5)	428	300
	Fontainebleau	15	13	7.1 (7.1)	123.3 (29.8)	132	444
	Haut Tuileau	7	7	4.7 (3.8)	24.6 (5.6)	164	127
	Rambouillet	8	8	7.4 (6.0)	11.8 (4.6)	168	115
	Verrières	4	4	9.0 (4.2)	51.0 (NA)	173	42
Mountains	Ballons-Comtois	8	8	9.8 (4.3)	26.4 (5.1)	1013	274
	Chartreuse	5	5	NA	NA	1278	50
	Ecouges	5	5	NA	NA	1148	248
	Engins	5	5	NA	100.0 (NA)	1581	190
	Haute Chaîne du Jura	8	7	10.1 (4.7)	29.6 (12.8)	816	2130
	Lure	4	4	23.8 (17.7)	40.3 (17.5)	1463	553
	Ventoux	5	5	16.3 (7.5)	98.4 (46.1)	1343	907
	Ventron	4	4	2.3 (1.2)	18.8 (0.5)	933	397
Totals and Means		114	108	8.5 (7.1)	47.7 (40.9)		

Tableau 16 : Site characteristics and sample sizes. n = number of plots; SD = standard deviation; MAN = managed forests; SFR = strict forest reserves); ha = hectares. NA= data not available.

Tree microhabitat inventories and metrics

Following the protocol described in Paillet *et al.* (2015b), we visually inspected for microhabitats all living trees (DBH ≥ 30cm) comprised within a fixed 2% relascopic angle in lowlands (resp. 3% in mountains) and standing dead trees (*i.e.* snags with DBH ≥ 30cm, excluding stumps with a height ≤ 1 m) comprised within a 20m radius from the plot center. The final sample thus included 2856 living trees and 170 snags distributed over the 222 plots. We recorded the presence of 28 microhabitat types (Tableau 17) based on the list published by Vuidot *et al.* (2011). To limit potential observer bias (Paillet *et al.*, 2015a), all censuses were performed by one and the same observer (Y.P.), except for one site (F.G.).

To calculate microhabitat density, we first counted the number of trees per plot bearing a given microhabitat type: if a tree bore several microhabitat types, the tree was counted once for each different microhabitat type; if the same microhabitat was found several times on a single tree, it was counted only once. The total microhabitat density per hectare therefore corresponds to the sum of microhabitat-bearing trees extrapolated to one hectare.

Preliminary data exploration revealed that some microhabitat types were underrepresented in the dataset (*e.g.* lightning scars), so we pooled several types into coherent morphological and functional groups (namely "microhabitat groups", Tableau 17) for subsequent analyses. The density of bearing trees was then calculated for each microhabitat group.

Microhabitat types	Occurrence (%, n=222)	Microhabitat groups
1. Presence of a crown skeleton (snags only)	15.8	Crown skeletons
2. Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown	36.5	
3. Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown	11.3	Crown deadwood
4. >50% of dead crown: one or more main branches are dead. The living crown appears to be <50% of the former total crown	9.9	
5. Broken stem: the primary crown is totally absent with or without the presence of a secondary crown. Main parts of the tree stem are already dead and decomposing	8.1	
6. Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch has resulted in severe damage to the main stem	9.9	Broken tops
7. Splintered stem: splitting has resulted in numerous slabs (minimum 5) of wood >50 cm long	5.0	
8. Conks of fungi. Fruiting bodies, diameter > 5cm.	12.6	
9. Conks of fungi. Equal to or more than 3 fruiting bodies >5 cm in diameter	10.8	Conks of fungi
10. Conks of fungi occurring in 10 cm long cascades of small fruiting bodies	11.3	
11. Non-woodpecker cavities with >5cm aperture: formed after injury, branch fall.	42.3	Non-woodpecker cavities
12. Woodpecker cavities with >2 cm aperture.	18.0	Woodpecker cavities
13. Cavity string: at least three woodpecker cavities on a same stem with a maximum distance of two meters between two cavity entrances	3.6	
14. Deep stem cavities: a tubular cavity in the base of the tree.	10.4	Base cavities
15. Deep stem cavities: a tubular cavity in the base of the tree with mould.	7.7	
16. Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	0.9	Cracks
17. Cracks: cleft in the sapwood >25 cm long along the stem and at least 2 cm deep	55.4	
18. Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 cm × 5 cm × 2 cm	58.6	
19. Bark pocket with mould: same structure and size as 17. but with mould	11.3	Bark characteristics
20. Bark loss: patches with bark loss of at least 5 cm × 5 cm mainly caused by injuries sustained from felling or natural falling of other trees	88.3	
21. Bark burst: black burst of bark often with resin indicating injury/disease	2.7	
22. Recent wood injury	3.6	
23. Canker: proliferation of cell growth; irregular cellular growth on stems or branches, caused by bark-inhabiting fungi, viruses or bacteria. Only cankerous areas >10 cm in diameter were recorded	25.7	Outgrowth
24. Witch broom: dense agglomeration of branches from a parasite or epicormic branching.	24.8	
25. Heavy sap or resin: fresh, heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size	11.7	Exudates
26. Sap or resin drop: Only a few sap or resin drops indicating a minor injury	12.6	
27. Bryophytes developed on >50% of the base (height <1m), trunk or branch area (noted separately)	74.8	Epiphytes
28. Ivy growing on >50% of the base (height <1m), trunk or branch area (noted separately)	20.7	

Tableau 17 : Microhabitat types, occurrences across plots and groupings

These densities were calculated for the total dataset, and for living trees and snags separately. For living trees, we also explored the relative contribution of the different DBH classes: we calculated the densities of microhabitats borne by very large trees (VLT, DBH ≥ 67.5cm), large trees (LT, 47.5 ≤ DBH < 67.5cm) and medium trees (MT, 30 ≤ DBH < 47.5cm).

Statistical analyses

We processed all the analyses with the R software v. 3.2.2 (R Core Team, 2015).

Management type (*i.e.* managed forest vs strict forest reserve) and time in years since the last harvesting were used as explanatory variables in separate analyses. We modelled the response of all microhabitat indices to these two variables with a linear mixed model within a Bayesian framework following the Markov Chain Monte Carlo (MCMC) methods in the MCMCglmm package (Hadfield, 2010). This package makes it possible to specify prior (*i.e. a priori*) distributions of the explanatory variables and uses MCMC methods instead of restricted maximum likelihood (REML). REML proved to be too sensitive to extreme values in our case; it was therefore impossible to apply the same methods as in Paillet *et al.* (2015b). Indeed, as our data contained a lot of zeros, traditional linear mixed model provided unreliable coefficient estimations.

We fitted our linear mixed models with a Gaussian error distribution since densities were count data extrapolated per hectare, which provided continuous data. As our sampling design was clustered (two plots in a given forest are more likely to be similar than two plots in two different forests), we used "forest" as a random factor in our analyses to take this source of spatial autocorrelation into account. We selected flat, uniform, non-informative priors for both fixed and random effects. For each model, we ran MCMC with 1 million iterations, a thinning of 50 iterations (*i.e.* one iteration in every 50 was kept for the estimation) and a burning period of 100,000 iterations (*i.e.* the 100 000 first iterations were discarded). We then visually assessed mixing and checked for autocorrelation within the remaining iterations. We assessed the significance of the differences between managed forests and strict forest reserves (resp. between slope and 0 for the analysis of time since last harvesting) with p-values based on Bayesian quantiles (Gosselin, 2011).

We first analysed the response of microhabitat densities to management type (n=222) and time since last harvesting (n=187) on the entire dataset. Then, as we expected responses to differ with elevation, we divided the dataset into two subsets and analysed the response to management type for lowland and mountain forests separately.

Results

Effects of management type

Total microhabitat densities

Microhabitat density was significantly higher in strict reserves than in managed forests for the entire dataset (+23%, Figure 7, Annexe 8). This pattern was mainly observed (and only significant) in mountain forests, with an even higher magnitude (+40%, Annexe 10). Total microhabitat density was higher for mountain forests, with levels in managed forests equivalent to those in lowland strict forest reserves. Densities for microhabitats on living trees tended to be higher in strict forest reserves than in their managed counterpart in mountain regions only (+25%) whereas no significant differences were detected for the entire dataset or for lowland forests (Figure 7, Annexe 8, Annexe 9). When divided into diameter classes, densities of microhabitats borne by very large trees were significantly higher in strict forest reserves than in managed forests for the entire dataset (+65%), a pattern mostly observed in mountain forests (+111%, Figure 8, Annexe 8 and Annexe 10). For the other diameter classes and forest types, we did not detect any significant difference (Figure 8, Annexe 8-10).

Densities of microhabitats on standing deadwood were consistently and significantly higher in strict forest reserves than in managed forests: entire dataset (+202%), lowland forests (+389%) and mountain forests (+183%, Figure 7, Annexe 8-10).

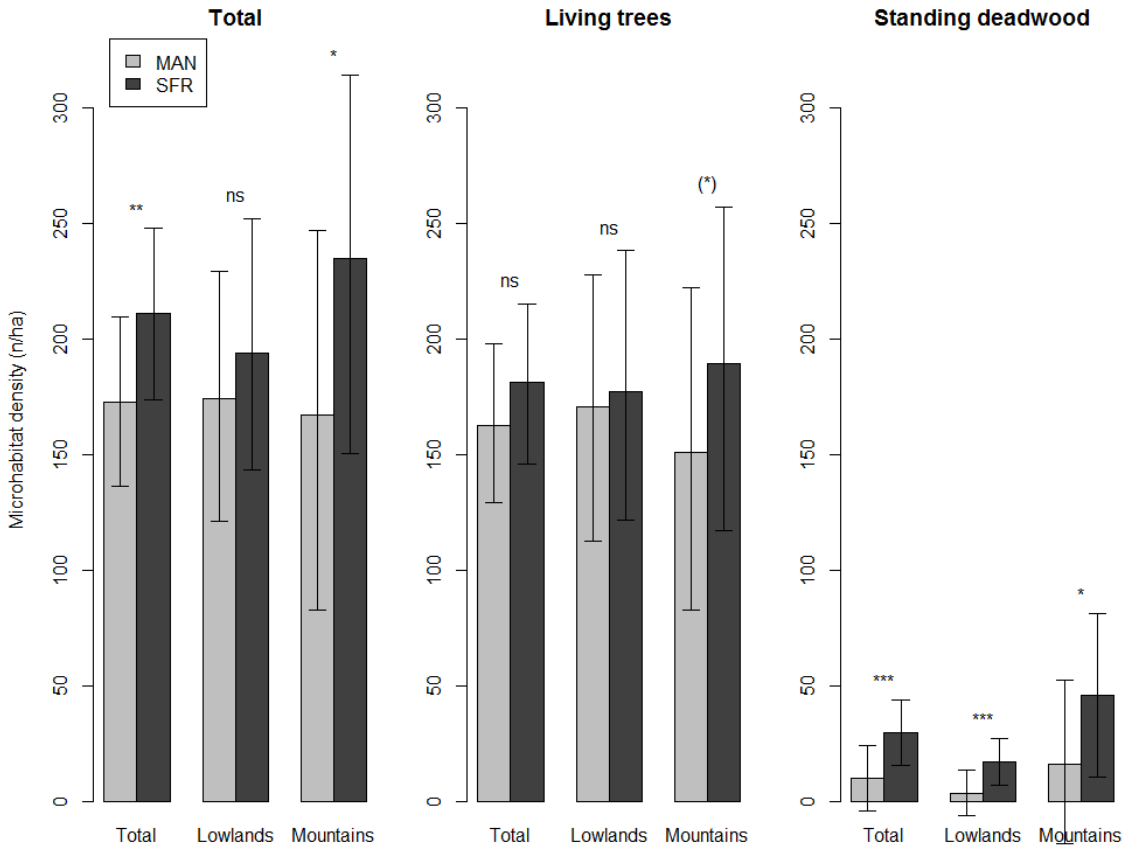


*Figure 7 : Comparison of microhabitat densities (ha^{-1}) between strict forest reserves (SFR) and managed (MAN) forests. Posterior means and 95% credibility intervals (error bars) are estimated by a linear mixed model with Gaussian error distribution and "forest" as a random factor fitted within a Bayesian framework (flat priors) using Markov Chain Monte Carlo methods; p = sampled posterior Bayesian p-value; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result. Note that credibility intervals comprising zero are due to MCMC estimations of the Gaussian error.*

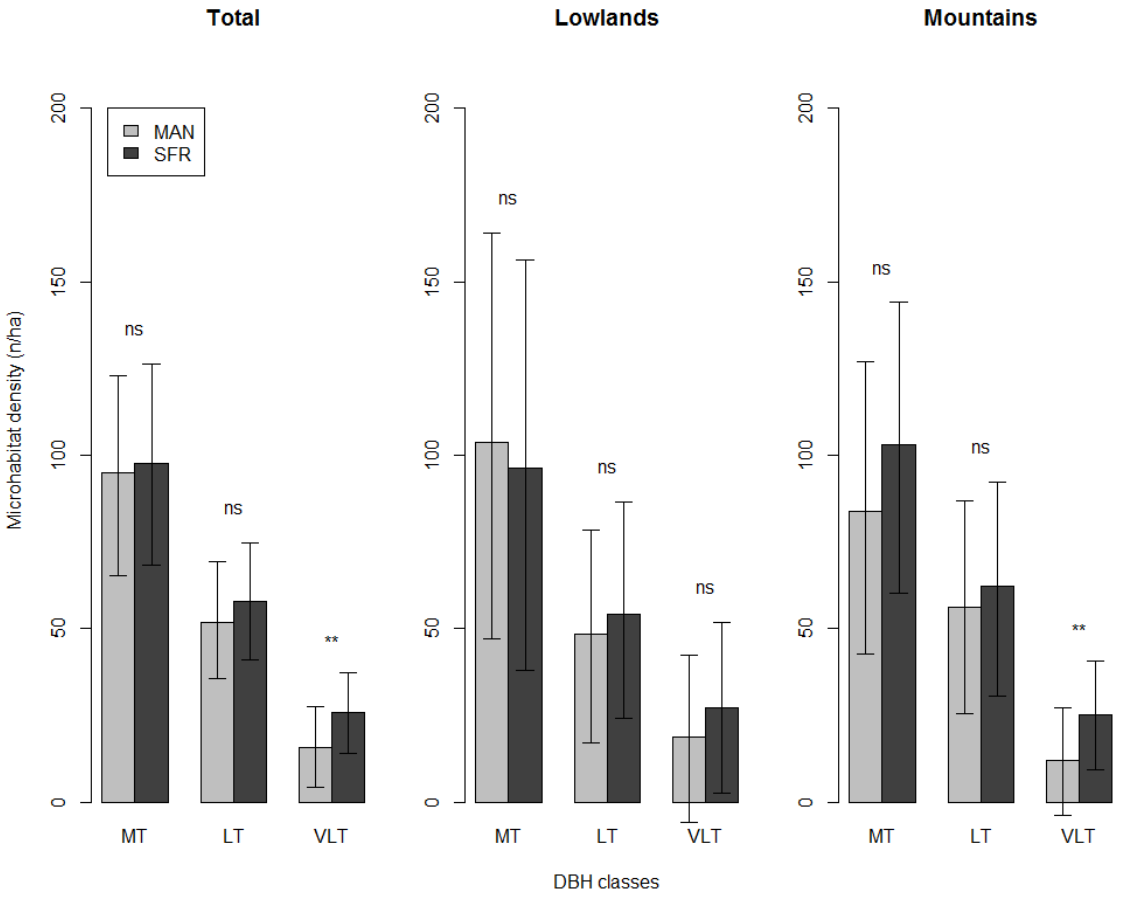


*Figure 8 : Comparison of microhabitat densities (ha^{-1}) for medium trees (MT, 30 ≤ DBH < 47.5cm), large trees (LT, 47.5 ≤ DBH < 67.5cm) and very large trees (VLT, DBH ≥ 67.5cm) between strict forest reserves (SFR) and managed (MAN) forests. Posterior means and 95% credibility intervals (error bars) are from a linear mixed model with Gaussian error distribution and "forest" as a random factor fitted within a Bayesian framework (flat priors) using Markov Chain Monte Carlo methods; p = sampled posterior Bayesian p-value; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result. Note that credibility intervals comprising zero are due to MCMC estimations of the Gaussian error.*

Individual microhabitat densities

For the entire dataset, most of the microhabitat groups had higher densities in strict forest reserves than in managed forests (Tableau 18a), with magnitudes ranging from +32% for epiphytes to +176% for broken forks (see Annexe 8 for absolute values). Only exudates had significantly lower densities in strict forest reserves (-53%) while conks of fungi, bark features and outgrowths were not significantly different. In lowland forests, the microhabitat group "woodpecker cavities" was the only group with significantly higher densities in strict forest reserves (+166%), all the other comparisons were not significant. In the mountain forests, five microhabitat groups out of ten showed significantly higher densities in strict forest reserves (Tableau 18a). Only exudates showed significantly lower densities in strict forest reserves than in managed forests (-65%), while conks of fungi, woodpecker cavities and outgrowths were not significantly different.

For living trees in the entire dataset (Tableau 18b), only non-woodpecker cavities, base cavities and epiphytes showed (marginally) higher densities in strict forest reserves forests, while exudates were significantly less dense in strict forest reserves (-55%). In lowland forests, none of these differences were significant, while in the mountains, non-woodpecker cavities and epiphytes had significantly higher densities in strict forest reserves than in managed forests. As for the entire dataset, exudates showed the opposite pattern. In addition, broken fork density was marginally lower in strict forest

reserves but the quasi absence of this microhabitat in managed mountains forests makes the result difficult to interpret. When divided into diameter classes and for the entire dataset, six out of eleven microhabitats groups borne by very large trees showed significantly higher densities in strict forest reserves (Tableau 18c, Annexe 8), but only two microhabitat groups for large (base cavities, +109% and exudates, -61%), and medium trees (exudates, -70% and epiphytes + 32%, Tableau 18c, Annexe 8) showed (marginally) significant differences. In lowland forests, only crown deadwood borne by very large trees (+202%), base cavities borne by large trees (+3453%) and bark characteristics borne by medium trees (-29%) showed significantly different densities (Tableau 18c, Annexe 9). In mountain forests, the densities of five microhabitat groups borne by very large trees were significantly higher in strict forest reserves (Tableau 18c, Annexe 10), while only two microhabitat groups borne by large trees (non-woodpecker cavities, +139% and exudates, -71%) and two borne by medium trees (exudates, -80% and epiphytes, 109%, Tableau 18c, Annexe 10) showed significant differences between strict forest reserves and managed forests.

For standing dead trees (Tableau 18d), all microhabitat groups except conks of fungi and exudates had significantly higher densities in strict forest reserves than in managed forests with magnitudes varying from +133% (crown skeleton) to +730% (epiphytes). In lowland forests, cracks were an exception, showing no significant difference. In mountain forests, only cracks (+316%), bark features (+167%) and epiphytes (+415%) had significantly higher densities in strict forest reserves. Note that, due to the scarcity of some microhabitat groups (notably for broken forks), some results were difficult to interpret in a robust way (see Annexe 8-10 for absolute values).

*Tableau 18 : Microhabitat density differences (%) between strict forest reserves (SFR) and managed (MAN) forests. The coefficient ([mean(SFR)-mean(MAN)]/mean(MAN)) represents the percentage of difference between strict forest reserves and managed forests with managed values as the reference: values are positive if the density is higher in strict forest reserves than in managed forests and negative if it is lower. DBH = Diameter at Breast Height; p = sampled posterior Bayesian p-value. ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result. Extreme coefficient values rise when the mean in managed forests is close to zero.*

a) All standing trees bearing microhabitats

Microhabitat group	Total	p	Lowlands	p	Mountains	p
Broken forks	176.2	*	104.9	ns	5207.2	(*)
Conks of fungi	-3.9	ns	-24.0	ns	53.8	ns
Woodpecker cavities	122.1	*	165.8	*	41.0	ns
Non-woodpecker cavities	66.4	*	37.2	ns	115.7	*
Base cavities	130.8	**	138.1	ns	151.9	*
Cracks	49.4	*	16.0	ns	111.0	*
Bark characteristics	11.5	ns	-2.8	ns	30.1	(*)
Outgrowths	-6.6	ns	5.0	ns	-20.4	ns
Exudates	-53.0	**	207.2	ns	-65.4	**
Epiphytes	31.5	**	14.3	ns	85.2	*

b) Living trees bearing microhabitats

Microhabitat group	Total	p	Lowlands	p	Mountains	p
Crown deadwood	40.0	ns	29.2	ns	73.2	ns
Broken forks	131.6	ns	68.0	ns	5207.2	(*)
Conks of fungi	-36.2	ns	-36.6	ns	5.5	ns
Woodpecker cavities	83.5	ns	111.2	ns	6.5	ns
Non-woodpecker cavities	53.3	(*)	18.4	ns	117.2	*
Base cavities	75.3	(*)	48.9	ns	100.8	ns
Cracks	26.3	ns	11.8	ns	56.5	ns
Bark characteristics	0.4	ns	-10.8	ns	15.8	ns
Outgrowths	-9.8	ns	0.9	ns	-22.1	ns
Exudates	-55.0	**	95.2	ns	-65.4	**
Epiphytes	27.9	*	11.7	ns	79.4	*

c) Living trees distributed by diameter classes

Diameter classes	Microhabitat group	Total	p	Lowlands	p	Mountains	p
Very large trees (DBH ≥ 67.5cm)	Crown deadwood	165.5	*	202.2	*	48.7	ns
	Broken forks	137.6	ns	120.9	ns	-	-
	Conks of fungi	43.5	ns	51.1	ns	-38.7	ns
	Woodpecker cavities	72.3	ns	90.0	ns	-17.7	ns
	Non-woodpecker cavities	174.1	**	83.6	ns	417.0	**
	Base cavities	55.1	ns	89.4	ns	49.9	ns
	Cracks	78.7	*	51.1	ns	174.7	*
	Bark characteristics	41.8	*	24.7	ns	75.3	(*)
	Outgrowths	100.7	*	40.4	ns	334.6	*
	Exudates	67.3	ns	96.4	ns	75.9	ns
	Epiphytes	59.9	*	35.0	ns	120.8	*
Large trees (47.5 ≤ DBH < 67.5cm)	Crown deadwood	26.6	ns	13.6	ns	63.2	ns
	Broken forks	253.5	ns	163.1	ns	3277.9	ns
	Conks of fungi	-29.7	ns	-47.6	ns	4942.1	ns
	Woodpecker cavities	98.0	ns	75.2	ns	174.3	ns
	Non-woodpecker cavities	58.5	ns	9.5	ns	139.1	*
	Base cavities	108.7	(*)	3453.2	*	49.6	ns
	Cracks	23.8	ns	8.1	ns	63.7	ns
	Bark characteristics	11.5	ns	14.2	ns	8.4	ns
	Outgrowths	-1.0	ns	41.0	ns	-42.5	ns
	Exudates	-60.5	**	344.1	ns	-71.1	**
	Epiphytes	10.5	ns	1.3	ns	29.1	ns
Medium trees (30 ≤ DBH < 47.5cm)	Crown deadwood	32.7	ns	19.6	ns	89.0	ns
	Broken forks	98.0	ns	31.5	ns	3166.5	ns
	Conks of fungi	-57.9	ns	-49.0	ns	-106.7	ns
	Woodpecker cavities	72.5	ns	226.4	ns	-103.9	ns
	Non-woodpecker cavities	30.6	ns	11.6	ns	66.3	ns
	Base cavities	56.4	ns	-36.7	ns	284.3	ns
	Cracks	7.7	ns	-11.3	ns	30.2	ns
	Bark characteristics	-12.0	ns	-29.1	*	12.8	ns
	Outgrowths	-36.4	ns	-34.0	ns	-39.2	ns
	Exudates	-69.9	*	25.9	ns	-79.9	**
	Epiphytes	32.0	(*)	13.1	ns	109.3	*

d) Standing dead trees bearing microhabitats

Microhabitat group	Total	p	Lowlands	p	Mountains	p
Crown skeletons	133.4	*	136.9	(*)	158.8	ns
Broken forks	2358.3	*	39673.7	*	-	-
Conks of fungi	72.3	ns	116.7	ns	65.8	ns
Woodpecker cavities	183.4	*	302.2	(*)	71.1	ns
Non-woodpecker cavities	312.1	**	1725.0	***	103.9	ns
Base cavities	3227.8	**	627.4	*	6856.9	*
Cracks	200.6	*	92.6	ns	316.3	*
Bark characteristics	188.3	**	421.2	**	166.8	*
Outgrowths	711.9	*	357.8	(*)	3154.3	ns
Exudates	805.7	ns	798.6	ns	-	-
Epiphytes	730.4	***	2503.6	**	414.5	*

Effects of time since the last harvesting

Total densities of microhabitats

For the entire dataset, the total density of microhabitats (combining living and standing dead trees, Figure 7a) and the density of microhabitats on standing dead trees only increased significantly with time since last harvesting (Annexe 11), with a higher magnitude for standing dead trees (+575% in 50 years for standing deadwood vs +19% for the entire dataset). The increase for living trees was not significant. When divided into diameter classes, only densities of microhabitats on very large trees for the entire dataset and lowland forests increased significantly with time since last harvesting (resp. +44% and +47%). The density of microhabitats on medium trees decreased marginally in lowland forests (-17%).

In lowland forests, only the density of microhabitat on standing dead trees increased significantly with time, with a slightly lower magnitude than for the entire dataset (+505% in 50 years, Annexe 12). In mountain forests, total density increased by +108% in 50 years and the density of microhabitats on standing dead trees increased by +333% (Annexe 13).

Individual microhabitat densities

When considering the entire dataset (living and dead trees), the densities of five microhabitat groups out of ten increased significantly with time since last harvesting, the lowest magnitude being observed for bark features (+18% in 50 years, marginal increase), and the highest for woodpecker cavities (+547%, Annexe 11). In the lowlands, the densities of three groups increased significantly: broken forks (+252% in 50 years), woodpecker cavities (+608%, Figure 9b) and base cavities (+652%). In the mountains, the densities of three groups increased significantly as well: broken forks (+260%), cracks (+3148%) and bark features (+88%).

For living trees, on the entire dataset, the densities of only three groups increased significantly with time: broken forks (+294% in 50 years), woodpecker cavities (+513%) and cracks (+29%, marginally). In the lowlands, the densities of broken forks (+158%), woodpecker cavities (+568%) and base cavities (+5000%) increased significantly. In the mountains, the densities of broken forks (+260%, marginally), crown deadwood (+852%) and cracks (+177%) increased significantly. When divided into diameter classes, the densities of four microhabitat groups borne by very large trees increased significantly with time since last harvesting: crown deadwood (+357% in 50 years), broken forks (909%), woodpecker cavities (+178%) and non-woodpecker cavities (+102%, Annexe 11). For large trees, only broken forks

(+714%), woodpecker cavities (+5000%) and exudates (+200%) showed significantly increasing densities with time since last harvesting. For medium trees, we did not observe any significant variation with time. The pattern was relatively similar in lowland forests, where five microhabitat groups on very large trees, three groups on large trees, and only two on medium trees showed (marginally) significantly increasing densities with time since last harvesting (Annexe 12). Conversely, in mountain forests, no group on very large trees showed (marginally) significant density increase, while four groups on large trees and two on medium trees did (Annexe 13).

For standing dead trees, the densities of microhabitats increased (marginally) significantly with time, with a few exceptions: conks on the entire dataset, crown skeleton, cracks and outgrowths in the lowlands, and conks and woodpecker cavities in the mountains. Magnitudes were usually higher than for either the entire dataset or living trees only (Annexe 11-13).

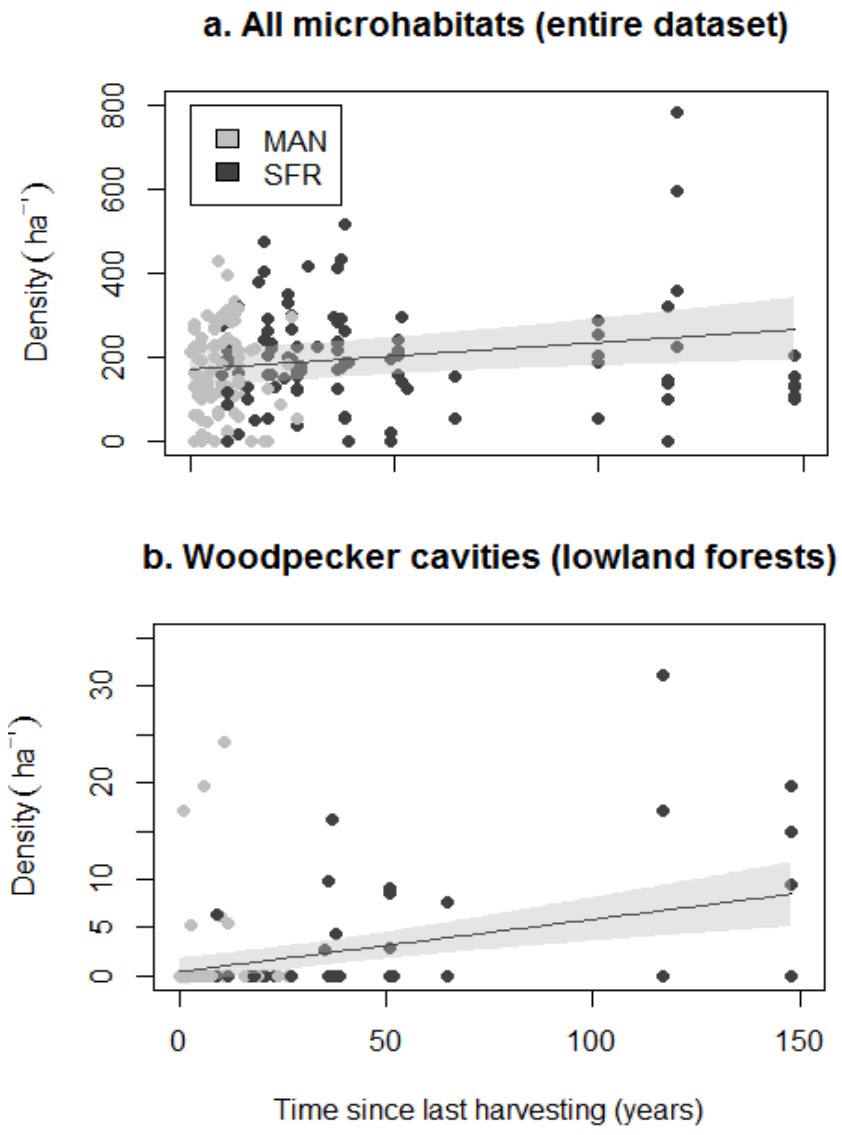


Figure 9 : Effect of time since last harvesting on (a) total microhabitat density and (b) the density of woodpecker cavities in lowlands. The plain line represents the posterior mean. The grey region represents the 95% credibility interval. SFR: strict forest reserves; MAN: managed forests.

Discussion

Higher microhabitat densities in strict forest reserves

Our comparisons based on a nationwide sampling – though restricted to lowland oak-beech-hornbeam and mountain beech-fir-spruce stands – support our hypothesis that strict forest reserves generally show higher microhabitat densities than comparable adjacent managed forests, either in terms of total or individual densities. Our results corroborate the general trend already observed in several relatively similar European forests, regardless of the protection status, *e.g.* in German beech forests (Winter and Möller, 2008; Winter *et al.*, 2015). Winter and Möller (2008) found that the abundance of microhabitats was roughly 2.5 times higher in their long abandoned plots compared with managed or recently abandoned ones. Similarly, Regnery *et al.* (2013) showed that recently harvested Mediterranean oak forests tended to have fewer microhabitats than similar forests where harvesting was older. However, Larrieu *et al.* (2012) found a higher total number of microhabitats in managed forests, though this was mainly due to the over-representation of certain types (bark loss, dendrotelms) in managed forests. The differences we observed in our study are relatively comparable to the differences found in the above-mentioned studies, despite the variations in the magnitudes observed. It is more difficult to compare absolute density values because we used different indices (density of microhabitat-bearing trees vs true microhabitat abundance). Furthermore, and perhaps most importantly, the different lists currently used for microhabitat censuses need to be reduced to a coarser grain to make comparisons possible (Larrieu *et al.*, 2014b), and this in turn would reduce the precision of the census. As a consequence, only our results for the density of individual microhabitats can be interpreted with respect to other international references. As mentioned in the introduction, cavities are by far the most documented microhabitat type. Remm and Lõhmus (2011) found a median density of 16 ha^{-1} cavities (either excavated or decayed) worldwide, while the mean density was lower for Palearctic regions (5.6 ha^{-1}). Our results showed higher cavity abundances, in both strict forest reserves and managed forests, even though we measured the density of cavity-bearing trees only (notwithstanding the number of cavities they bore) which underestimates true cavity density. This difference may be due to the fact that these authors included in their analyses a significant amount of studies carried out in boreal forests, where cavity densities are generally lower (Remm and Lõhmus, 2011, Michon, 2014, but see Ouellet-Lapointe *et al.*, 2012 for Nearctic regions). One could also assume that some reserves have been designated on purpose in areas already displaying old-growth characteristics or high microhabitat densities, but no evidence of such a possible bias could be found in the available documentation.

For microhabitats other than cavities, only some can be compared with the literature, but remain generally poorly covered. For conk-bearing trees, Bouget *et al.* (2013) found between 0.9 and 1.3 ha^{-1} in oak and beech forests in France, based on a rapid habitat assessment and a sampling design partly overlapping with ours. On a larger sample across France including lowland and mountain forests, Bouget *et al.* (2014a) mentioned 0.9 conk-bearing trees per hectare, which is largely below the densities we found (3.3 and 3.1 conk-bearing trees in managed forests and strict forest reserves, respectively). However, their sample included 75% of recently harvested forests, which may explain the discrepancy with our results. On the other hand, the densities of crown deadwood-bearing trees estimated in Bouget *et al.* (2014a) were close to the ones we observed; their mean densities were roughly 5 to 8 trees per hectare, vs 8.5 to 12 per hectare in our entire dataset. Despite these similarities, it is clear that these estimations should be confirmed by other studies which clearly differentiate values for different forest types and ecological conditions.

Compared to lowland forests, we found that mountain forests had higher densities of microhabitats and stronger (and also more often significant) differences between managed forest and strict forest reserves. Higher values in mountains have already been observed for other structural data, especially old-growth attributes, such as amount of deadwood and large trees (Paillet *et al.*, 2015b). However, Paillet *et al.* (2015b) showed greater differences between managed forests and strict reserves in lowland forests due to the scarcity of large trees and deadwood in managed forests. They argued that

the stronger effect of harvesting on old-growth attributes in lowland forests was due to the more intensive practices carried out there. This argument does not seem to hold for microhabitat densities, for which differences between managed forests and strict forest reserves are larger in mountain forests. Indeed, the production of microhabitats seems higher in mountain forests as shown by higher microhabitat densities in strict forest reserves in mountain compared with lowlands, notably bark characteristics, exudates and outgrowths. A tree species effect for these microhabitats cannot be totally ruled out here since we did not sample coniferous species in lowlands and some microhabitat types are species-specific (*e.g.* resin-drops). In addition, topography and climatic conditions may also play a role. In particular, steep slopes favouring rockfalls and higher atmospheric moisture levels – as well as harsher climatic conditions including snowfall and frosts – may favour the production of microhabitats linked with tree decline and decaying processes (*e.g.* Remm and Lõhmus, 2011 for cavities). Finally, higher selection towards trees bearing defects, especially on very large – and valuable – trees in mountains forests cannot totally be ruled out, but such effect remains unclear.

The central role of snags and large trees

The density of microhabitats borne by snags was four times lower than the density of microhabitat borne by living trees (Figure 7). However snags over-contributed to the difference between managed forests and strict forest reserves, with three times more microhabitat-bearing snags in strict forest reserves for the entire dataset. Indeed, the higher occurrence of snags in strict forest reserves (Paillet *et al.*, 2015b) induced greater differences in microhabitat densities. This once again confirms the role of standing dead trees in providing microhabitats, either in terms of total number (Vuidot *et al.*, 2011), diversity or for specific microhabitat types (Larrieu *et al.*, 2012). Similarly, the density of microhabitats borne by very large trees (DBH ≥ 67.5 cm) was almost eight time lower than the densities borne by the other tree diameter categories, but the density of very large microhabitat-bearing trees was 65% higher in strict forest reserves than in managed forests. Despite their lower overall densities, the contribution of larger trees to this difference is thus non-negligible, although it does not reach the levels observed for snags. Larger – and most of the time older – trees have a longer life history and consequently more chances to be exposed to events generating microhabitats (*e.g.* storms, frost, rock fall…). Large trees also provide buffered microclimatic conditions for a broad diversity of cavity nesters (*e.g.* Cockle *et al.*, 2010; Cockle *et al.*, 2011; Edworthy and Martin, 2013). As a consequence, cavity builders tend to excavate cavities preferentially on larger trees.

Microhabitat densities increase with time since last harvesting

In line with Paillet *et al.* (2015b), we found that densities of microhabitat-bearing trees increased with time since last harvesting regardless of the forest type (lowland or mountain forests), but that the dynamics differed among microhabitat types. Again, this result was more pronounced for snags than for living trees. Accumulation rates were roughly of the same order of magnitude to those of old-growth attributes observed elsewhere (see discussion in Paillet *et al.*, 2015b, and references therein). However, contrary to old-growth attributes, studies on accumulation rates for microhabitats remain rare, or are limited to certain types of microhabitats. Once again, cavities have been studied most frequently (*e.g.* Cockle *et al.*, 2010), but even here, accumulation rates remain poorly documented for temperate forests. We found that there was an effect of time since last harvesting for woodpecker and base cavities on living trees. This is very probably due to the larger proportion of large or very large trees in strict forest reserves (Paillet *et al.*, 2015b). Indeed, in our dataset, microhabitats borne by very large trees also showed increasing densities with time since last harvesting, notably on the entire dataset and in lowland forests. Time series on microhabitat types other than cavities are virtually non-existent, but we can assume that their accumulation rate is also mainly driven by the accumulation rate of snags and tree growth (Vuidot *et al.*, 2011), as shown by the larger proportion of significant

results we obtained for snags and very large trees (see Annexe 11-13). Finally, our study estimates accumulation rates for a set of microhabitats with a space-for-time substitution approach. Although imperfect, this approach provides an insight into microhabitat dynamics on a large biogeographical gradient including several forest types at a national scale (see also Larrieu *et al.*, 2014b for mountain forests).

Despite these results, many microhabitat groups did not vary with time since last harvesting, most surprisingly conks of fungi. This could be linked to a slower dynamics for these microhabitats than for the others or to other overlooked drivers like, *e.g.* forest continuity, the signal of which could not be detected in our dataset. Indeed, we worked on a rather small gradient of management abandonment (*i.e.* 0 to 150 years since last harvesting) and the intensity of management in managed forests may be considered relatively low compared to other more intensive systems (*e.g.* plantations, see discussion in Paillet *et al.*, 2015b). The accumulation of microhabitats may not even be linear, but rather exponential, logistic or cyclical, a form that is not assumed by the models we used and that remains to be tested.

Perspectives for research and implications for forest management and biodiversity conservation

The present study should be viewed as one of the first to provide quantitative data on microhabitat densities for France and it is complementary to other studies already published for other forest types and biogeographic regions in France and Europe (Bouget *et al.*, 2013; Bouget *et al.*, 2014a; Larrieu *et al.*, 2014b; Winter *et al.*, 2015). Given the heterogeneity of the results obtained among these studies, it is now important to standardize microhabitat censuses as much as possible to overcome methodological differences that make comparisons difficult. The first step in this direction would be to propose a hierarchized typology of microhabitat types, with nested types allowing managers and researchers to inventory microhabitats at various grains (see notably the initiative of Kraus *et al.*, 2016). Future studies should clearly specify the indices used to estimate microhabitat densities at the plot scale (*e.g.* true abundance vs microhabitat-bearing tree densities). Finally, standardized operating protocols should be implemented and tested to limit a potentially strong observer effect to detect small structures, some of which being frequently located in the upper tree trunks or high in the canopy and hardly visible from the ground (Paillet *et al.*, 2015a). Such conditions are prerequisites to allow generalisations of microhabitat censuses, in particular in national forest inventories, and to implement forest biodiversity indicators (Gao *et al.*, 2015; Zellweger *et al.*, 2015). Creating large databases of microhabitat censuses would make the study of relationships with biodiversity easier, especially for rare features (*e.g.* sap runs) that may play an important role for rare or specialized species.

Although the approach with time since last harvesting provides estimates of microhabitat accumulation rates with time, only long-term monitoring of permanent plots at *e.g.* 5-10-year intervals would be an efficient way to better understand accumulation dynamics, at the tree (Edworthy and Martin, 2014) and plot scales (Larrieu *et al.*, 2014b). In particular, it could be interesting to analyse the effects of succession and tree species replacement on microhabitat densities. As succession may not be unidirectional, it may thus help to better define guidelines for biodiversity-friendly management methods that might better take into account successional stages than the current approach. Such inventories – including surveys of microhabitats – are currently being implemented on the monitoring network of the French forest reserves and the data collected will hopefully help us better understanding microhabitat dynamics.

The present study not only feeds the scientific references on microhabitat densities for European and French forests but also provide information about the occurrence of the various types of microhabitats in managed stands. Our comparison of managed forests with relatively recently abandoned strict forest reserves shed light on the impacts of silviculture on the microhabitats profile. It may thus inspire forest managers to include microhabitat conservation in their forestry practices such as tree

designation for thinning or habitat trees conservation. The levels of microhabitat densities we measured in strict forest reserves, though imperfect and limited to some forest types, could help forest managers to evaluate the current target values that were consensually defined, and provide evidence for a revision of these targets. Our results point toward increasing the number of habitat trees in managed stands, especially snags and large trees that harbour a variety of microhabitats (Bütler *et al.*, 2013). One should bear in mind that some higher values may not be attainable in managed forests where quality wood production is the main target; these targets may only be achievable in strict forest reserves. At the landscape scale, it is now critical to identify the density and diversity of microhabitats types that are essential in managed stands to provide a functional matrix for the conservation of species relying on these structures.

Finally, research more directly targeting the link between biodiversity and microhabitat densities will be a major source of inspiration for biodiversity-friendly forest management. Such research could help to disentangle the effects of *e.g.* deadwood or large trees as such, with effects of microhabitats within a multitaxonomic approach. In the end, such analysis may help define the best proxy – or combination of proxies – for biodiversity assessment (Bouget *et al.*, 2013).

Acknowledgements

This project would not have been possible without a strong commitment by field managers and their willingness to contribute to this research. We are indebted to J-J. Boutteaux (ONF, Auberive), S. Ducroux (ONF, Fontainebleau), L. Domergue (RN Ventron), L. Lallement and S. Coulette (ONF, RN Ballons-Comtois), R. Leconte (RN Chalmessin), L. Servières (RN Combe-Lavaux), B. Blaise (ONF Citeaux), D. Barré (ONF Chizé), B. Fritsch (RN Bois du Parc), J. Leseure (ONF Haut-Tuileau), J. Terracol and E. Jensel (ONF Ventoux), D. Reboul and J-P. Golé (ONF Lure), E. Royer and J-L. Témoin (ONF Rambouillet), G. Sivry (ONF Verrières) and S. Dumas (ONF Jura), S. Pauvert, J. Rosset and H. Tournier (RN Haute Chaîne du Jura) for their constant help and fieldwork coordination. Comments from two anonymous reviewers helped to improve the manuscript. We also thank V. Moore for language editing. This research was funded by the French Ministry in charge of Ecology (Convention Cemagref-DEB (MEEDDAT), Action GNB and the program “Biodiversité, Gestion Forestière et Politiques Publiques” (BGF), convention GNB 10-MBGD-BGF-1-CVS-092, no CHORUS 2100 214 651) and the Office National des Forêts (Convention ONF-Cemagref, Action 5, 2008).

References cited

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For Ecol Manag 258, 525-537.

Bollmann, K., Braunisch, V., 2013. To integrate or to segregate: balanding commodity production and biodiversity conservation in European forests. In: Kraus, D., Krumm, F. (Eds.), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg, Germany, pp. 18-31.

Bouget, C., Larrieu, L., Brin, A., 2014a. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecol Indic 36, 656-664.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers Conserv 22, 2111-2130.

Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L., Gosselin, F., 2014b. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Anim Conserv.

Bütler, R., Lachat, T., Larrieu, L., Paillet, Y., 2013. Habitat trees: key elements for forest biodiversity. In: Kraus, D., Krumm, F. (Eds.), Integrative approaches as an opportunity fir the conservation of forest biodiversity. European Forest Institute, Freiburg, DEU, pp. 84-91.

Christensen, M., Hahn, K., Mountford, E.P., Odor, P., Standovar, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. For Ecol Manag 210, 267-282.

Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol Conserv 143, 2851-2857.

Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9, 377-382.

Drapeau, P., Nappi, A., Imbeau, L., Saint-Germain, M., 2009. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. Forestry Chronicle 85, 227-234.

Edworthy, A.B., Martin, K., 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. J Wildl Manag 77, 770-776.

Edworthy, A.B., Martin, K., 2014. Long-term dynamics of the characteristics of tree cavities used for nesting by vertebrates. For Ecol Manag 334, 122-128.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For Ecol Manag 155, 399-423.

Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol Indic 57, 420-434.

Gosselin, F., 2011. A new calibrated bayesian internal goodness-of-fit method: Sampled posterior p-values as simple and general p-values that allow double use of the data. PLoS ONE 6.

Gustafsson, L., Bauhus, J., Kouki, J., Lõhmus, A., Sverdrup-Thygeson, A., 2013. Retention Forestry – an integrated approach in practical use. In: Kraus, D., Krumm, F. (Eds.), Integrative approaches as an opportunity fir the conservation of forest biodiversity. European Forest Institute, Freiburg, DEU, pp. 74-81.

Hadfield, J.D., 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software 33, 22.

Jackson, J.A., Jackson, B.J.S., 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor 106, 37-49.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., Winter, S., 2016. Catalogue of tree microhabitats – Reference field list. In. Integrate+ Technical Paper, European Forest Insitute, Freiburg, Germany.

Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg, Germany.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can J For Res 42, 1433-1445.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014a. Tree microhabitats at the stand scale in montane beech-fir forests: Practical information for taxa conservation in forestry. European Journal of Forest Research 133, 355-367.

Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. European Journal of Forest Research 131, 773-786.

Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., Deconchat, M., 2014b. Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring. For Ecol Manag 334, 163-173.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11, 1027-1039.

Lombardi, F., Lasserre, B., Chirici, G., Tognetti, R., Marchetti, M., 2012. Deadwood occurrence and forest structure as indicators of old-growth forest conditions in mediterranean mountainous ecosystems. Ecoscience 19, 344-355.

Michon, S., 2014. Comparison of tree cavity abundance and characteristics in managed and unmanaged Swedish boreal forest. In, Department of Wildlife, Fish and Environmental Studies. Faculty of Forest Science, Umea, Sweden, p. 25.

Millenium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis. In, MEA. World Resources Institute, Washington, DC., p. 155.

Ouellet-Lapointe, U., Drapeau, P., Cadieux, P., Imbeau, L., 2012. Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of Eastern Canada. Ecoscience 19, 391-397.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F., Gosselin, F., 2015a. Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. Ecol Indic 49, 14-23.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015b. Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. For Ecol Manag 346, 51-64.

Parviainen, J., Bucking, W., Vandekerkhove, K., Schuck, A., Paivinen, R., 2000. Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). Forestry 73, 107-118.

R Core Team, 2015. R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria.

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? For Ecol Manag 295, 118-125.

Remm, J., Lõhmus, A., 2011. Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. For Ecol Manag 262, 579-585.

Siitonen, J., 2012. Microhabitats. In: Stokland, J.N., Siitonen, J., Jonsson, B.G. (Eds.), Biodiversity in dead wood. Cambridge University Press, New York, USA, pp. 150-182.

Tinner, R., Streit, K., Commarmot, B., Brang, P., 2012. Stichprobeninventur in schweizerischen Naturwaldreservaten - Anleitung zu Feldaufnahmen. In. Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmesndorf, Eidg., p. 44.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol Conserv 144, 441-450.

Winter, S., 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. Forestry 85, 291-304.

Winter, S., Höfler, J., Michel, A.K., Böck, A., Ankerst, D.P., 2015. Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. European Journal of Forest Research 134, 335-347.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For Ecol Manag 255, 1251-1261.

Zellweger, F., Braunisch, V., Baltensweiler, A., Bollmann, K., 2013. Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale. For Ecol Manag 307, 303-312.

Zellweger, F., Braunisch, V., Morsdorf, F., Baltensweiler, A., Abegg, M., Roth, T., Bugmann, H., Bollmann, K., 2015. Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests. For Ecol Manag 349, 36-44.

Chapitre 4 - Quantifier le lien avec la biodiversité

4.1. "The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles" – Paillet et al. J. App. Ecol. (2018).

RESEARCH ARTICLE

Journal of Applied Ecology

The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles

Yoan Paillet[1,2] | Frédéric Archaux[1] | Solène du Puy[1] | Christophe Bouget[1] | Vincent Boulanger[3] | Nicolas Debaive[3,4] | Olivier Gilg[4] | Frédéric Gosselin[1] | Eric Guilbert[2]

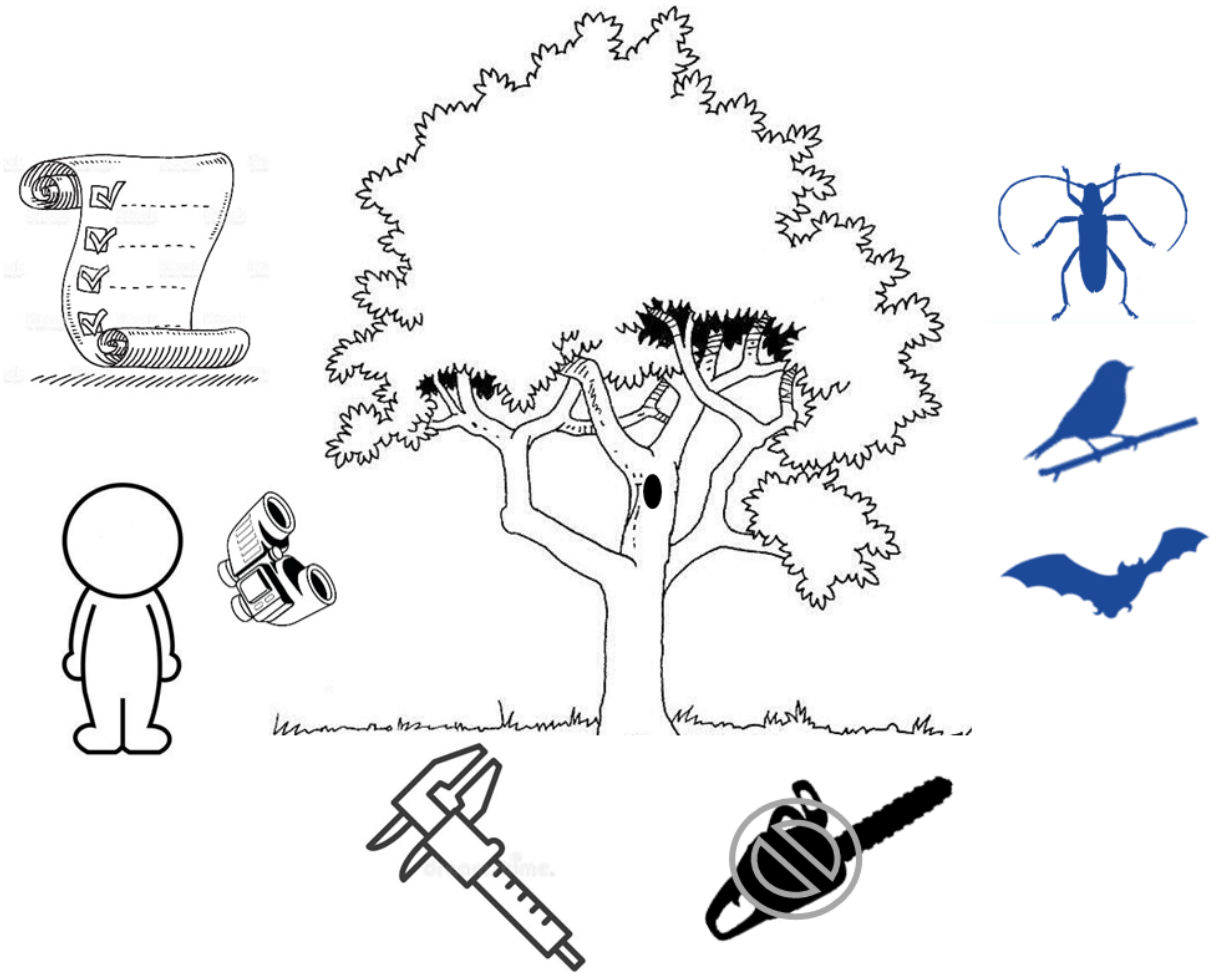
Résumé

1. L'évaluation de la biodiversité forestière aux niveaux national et international repose très largement sur des indicateurs indirects, basés sur des éléments de structure forestère utilisés comme substituts de la diversité d'espèces. Ces proxies sont réputés plus faciles et moins coûteux à évaluer que la biodiversité. Les microhabitats des arbres – des singularités portées par les arbres telles les cavités, les carpophores de champignon ou les caractéristiques de l'écorce – sont considérés comme des indicateurs potentiels de biodiversité. Cependant, comme beaucoup d'indicateurs de biodiversité, les connaissances scientifiques qui documentent leur lien avec la biodiversité qu'ils sont supposés indiquer sont lacunaires.

2. Nous avons exploré le lien entre indices de microhabitats et la richesse et l'abondance de trois groupes taxonomiques : les chauves-souris, les oiseaux et les coléoptères saproxyliques. Grâce à un plan d'échantillonnage national, nous avons comparé 213 placettes sitées dans et en dehors de réserves forestières intégrales en France. Nous avons fait l'hypothèse que l'effet positif de la mise en réserve sur la conservation de la biodiversité est indirectement dû à une augmentation de la proportion d'éléments de grandes dimensions (*e.g.* arbres vivants, bois mort debout et au sol). Ces éléments, par extension, ont tendance à favoriser la quantité et la diversité de microhabitats. Nous avons analysé les relations entre l'abondance et la richesse spécifique de différents groupes et guildes (*e.g.* espèces de listes rouges, specialistes forestiers, cavicoles) et la densité et la diversité des microhabitats. Nous avons ensuite utilisé des modèles d'équations structurelles pour évaluer les effets directs et indirects de l'abandon d'exploitation, des éléments de grandes dimensions et des microhabitats sur la biodiversité.

3. Pour plusieurs groupes d'oiseaux et de chauves-souris, nous avons montré une médiation par les microhabitats des effets indirects de l'abandon d'exploitation et des éléments de structure sur la biodiversité. Cependant, la magnitude du lien entre indices de microhabitats et biodiversité était modérée. En particulier, la biodiversité des coléoptères saproxyliques était mal expliquée que ce soit par les microhabitats, les éléments de grandes dimensions ou l'abandon d'exploitation.

4. *Synthèse et applications*. Les microhabitats des arbres peuvent être considérés comme indicateurs de la diversité des chauves-souris et des oiseaux, mais ne constituent pas un indicateur de biodiversité universel. En comparaison avec les éléments de structure, ils ont plutôt un rôle complémentaire sur la biodiversité. En termes de gestion forestière et de conservation, préserver une diversité de microhabitats à l'échelle locale bénéficie à plusieurs groupes de chauves-souris et d'oiseaux.



The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles

Running headline: Tree microhabitats as biodiversity indicators

Yoan Paillet[1,2*], Frédéric Archaux[1], Solène du Puy[1], Christophe Bouget[1], Vincent Boulanger[3], Nicolas Debaive[3,4], Olivier Gilg[4], Frédéric Gosselin[1], Eric Guilbert[2]

[1] Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France
[2] MECADEV, UMR 7179 MNHN/CNRS, CP50, 57 rue Cuvier, 75005 Paris, France
[3] Office National des Forêts, Département Recherche et Développement, Boulevard de Constance, 77300 Fontainebleau, France
[4] Réserves Naturelles de France, CS 67524, 21075 Dijon cedex, France
*Corresponding author: yoan.paillet@irstea.fr

Abstract

1. National and international forest biodiversity assessments largely rely on indirect indicators, based on elements of forest structure that are used as surrogates for species diversity. These proxies are reputedly easier and cheaper to assess than biodiversity. Tree microhabitats – tree-borne singularities such as cavities, conks of fungi or bark characteristics – have gained attention as potential forest biodiversity indicators. However, as with most biodiversity indicators, there is a lack of scientific evidence documenting their quantitative link with the biodiversity they are supposed to assess.
2. We explored the link between microhabitat indices and the richness and abundance of three taxonomic groups: bats, birds, and saproxylic beetles. Using a nation-wide multi-taxon sampling design in France, we compared 213 plots located inside and outside strict forest reserves. We hypothesized that the positive effect setting aside forest reserves has on biodiversity conservation is indirectly due to an increase in the proportion of large structural elements (*e.g.* living trees, standing and lying deadwood). These, in turn, are likely to favour the quantity and diversity of microhabitats. We analysed the relationship between the abundance and species richness of different groups and guilds (*e.g.* red-listed species, forest specialists, cavity dwellers) and microhabitat density and diversity. We then used confirmatory structural equation models to assess the direct and indirect effects of management abandonment, large structural elements and microhabitats on the biodiversity of the target species.
3. For several groups of birds and bats, the indirect effect of management abandonment and large structural elements on biodiversity was mediated by microhabitats. However, the magnitude of the link between microhabitat indices and biodiversity was moderate. In particular, saproxylic beetles' biodiversity was poorly explained by microhabitats, large structural elements or management abandonment.
4. *Synthesis and applications*: Tree microhabitats may serve as indicators for bats and birds, but they are not a universal biodiversity indicator. Rather, compared to large structural elements, they most likely have a complementary role to biodiversity. In terms of forest management and conservation, preserving diversity of microhabitats at the local scale benefits several groups of both bats and birds.

Keywords: bats; birds; saproxylic beetles; strict forest reserves; tree-related microhabitats; cavities; indicator; structural equation models.

Introduction

While warnings about the global decline in biodiversity are becoming increasingly alarming (Butchart et al., 2010), biodiversity assessment and monitoring remain a challenge in many ecosystems around the world (Lindenmayer & Likens, 2010). Despite the recent implementation of large-scale initiatives, such as GEOBON (Scholes et al., 2012), scientifically validated tools and indicators assessing the extent of this loss are limited. In European forests, most biodiversity indicators are based on data from national forest inventories (Chirici et al., 2012) which were historically designed to assess wood production at a large scale. For instance, the State of Europe's Forest assessment (Forest Europe, 2015a) mostly relies on forest structure indices as surrogates for biodiversity conservation (aka. indirect indicators) which assume that greater diversity and abundance of species are associated with larger quantities of suitable habitat. Direct measures of biodiversity are restricted to red-listed species and, for the upcoming reporting in 2020, breeding birds (see Forest Europe, 2015b). Indirect (structural) biodiversity indicators have obvious practicality assets: they are generally cheaper and easier to assess than biodiversity itself. However, it is likely that a non-negligible proportion of these surrogates, defined in different political or management contexts, is based on "anecdote and myth rather than scientific evidence" (Sutherland et al., 2004). Therefore, clear evidence-based definitions of biodiversity indicators are still needed (Gao et al., 2015).

The panel of tools used to conserve biodiversity includes set-asides (strict forest reserves, Parviainen & Frank, 2003) and the maintenance, either in managed or unmanaged forests, of large structural elements (habitat trees, standing and lying dead trees) that are likely to support a specific biodiversity (see Bütler et al., 2013). Set-asides, as well as large structural elements, are generally rare in European forests, since most of the surface is currently being managed for wood production (Parviainen & Frank, 2003), which tends to eliminate large structural elements characteristic of overmature or senescent phases of the forest cycle (Paillet et al., 2015b). Furthermore, current strict forest reserves have experienced various human uses in a more or less recent past, such as wood harvesting. Hence, it is quite difficult to disentangle the respective roles of this management abandonment, following past harvesting in the present strict forest reserves, and large structural elements. Indeed, management abandonment generally induces higher occurrence and greater quantities of large structural elements (Bouget et al., 2014b; Paillet et al., 2015b; Vandekerkhove et al., 2009). In turn, it is not clear whether management abandonment per se – as a complex combination of structure modifications, landscape features and low levels of human disturbance – or the modifications of the forest structure only, is responsible for the observed increase in the biodiversity of certain taxa (notably those dependent on deadwood, Paillet et al., 2010). In addition, large trees are likely to bear peculiarities – including cavities, cracks, conks of fungi or bark features: since they are older, they are also more prone to damages (storm, rockfall), decay processes and modification by foraging species such as woodpeckers (Larrieu & Cabanettes, 2012; Regnery et al., 2013b; Vuidot et al., 2011). Such tree-related microhabitats (Larrieu et al., 2018, hereafter microhabitats) potentially provide a necessary substratum for certain taxa during at least a part of their life cycle, notably cavity-dwelling birds, bats and saproxylic insects (Larrieu et al., 2018; Paillet et al., 2017; Redolfi De Zan et al., 2014). That is why microhabitats have recently gained scientists' attention as biodiversity indicators, with a potentially better, or complementary role, compared to indicators classically used in forest monitoring such as deadwood and large trees (Bouget et al., 2014a; Larrieu et al., 2018 but see ; Pierson et al., 2015). While the link between biodiversity and some microhabitat types has been documented (Larrieu et al., 2018), most of this knowledge is based on naturalist expertise or case studies generally involving a single species group (*e.g.* Bouget et al., 2014a for saproxylic beetles; Regnery et al., 2013a for birds and bats; and Tillon et al., 2016 for bats). Correlative multi-taxon or multi-group studies linking biodiversity and microhabitat lists remain rare. In addition, studying the response of different guilds (*e.g.* forest specialists) or different biodiversity metrics (species richness, abundance, or occurrence) may help us better understand the underlying ecological mechanisms involved. In this sense, the potential link between microhabitats and different taxa with similar ecological preferences (*e.g.* forest specialists or cavity dwellers) has, to our knowledge, never been explored.

In this context, we analysed the relationship between management abandonment, large structural elements (living trees, standing and lying deadwood) and microhabitats on one hand, and biodiversity on the other. We used a nationwide dataset and a multi-taxon sampling design, comparing 213 plots located inside and outside forest reserves in France, to explore the link between microhabitat indices and the richness and abundance of three taxa (bats, birds, and saproxylic beetles). We hypothesized that the positive effect of management abandonment on biodiversity was indirectly due to the increase in the quantity of large structural elements, which in turn favoured the quantity and diversity of microhabitats. Microhabitats would thus have a more direct – functional – role than large structural elements on biodiversity. Using structural equation models, we tested whether microhabitat indices mediate the effects of management abandonment and large structural elements. We also hypothesize that this effect would depend more on ecological affinities (*e.g.* forest specialists, shade-tolerant species, cavity dwellers) rather than on taxonomy. In other words, we thus assumed that tree microhabitats could constitute a more direct – or complementary – biodiversity indicator than large structural elements or management abandonment.

Materials and methods

Study sites, stand structure description and tree microhabitat inventories

We compared fifteen strict forest reserves distributed across France (Tableau 19) with adjacent managed forests under the same site conditions (213 plots, see Paillet et al., 2015b for a thorough description of the sampling design, and Annexe 14 for a summary of the main characteristics). Forest types comprised mixed oak-beech-hornbeam forest in lowlands, and mixed beech-fir-spruce in mountains. On each plot (surface area of ca. 0.12ha), we quantified all living and standing dead trees (*i.e.* snags, excluding stumps with a height ≤ 1 m, Paillet et al., 2015b) with a Diameter at Breast Height (DBH) above 30cm and visually inspected them for tree microhabitats (the typology of which follows Paillet et al., 2017). The main microhabitat groups inventoried were: tree crown skeletons, crown deadwood and broken tops; conks of fungi; base, non-woodpecker and woodpecker cavities; cracks; bark characteristics; outgrowths; exudates and epiphytes (see Annexe 14). We also quantified all lying dead trees (*i.e.* logs) with a diameter larger than 30cm.

Based on these measurements, we derived three stand structure descriptors: (i) Basal area of large living trees (DBH ≥ 47.5cm); (ii) Volume of large snags (DBH ≥ 47.5cm); and (iii) Volume of large logs (Diameter ≥ 47.5cm). We also calculated seven microhabitat densities (abundance per hectare, see Paillet et al., 2017 for calculation method): (i) total microhabitat density based on the number of trees bearing at least one microhabitat type; (ii) density of living trees bearing at least one microhabitat type; (iii) density of snags bearing at least one microhabitat type; (iv) density of living trees or snags bearing at least three microhabitat types; (v-vii) densities of trees bearing either cracks, cavities or conks. Finally, we calculated a microhabitat diversity index as follows: for each tree, we combined microhabitat types and tree species to create a combination per tree, for both living trees and snags (*e.g.* oak + conk, oak + conk + cavity, etc.). The microhabitat diversity index is the sum of the different combinations per plot. We calculated this index for (i) living trees and snags combined, (ii) living trees only, and (iii) snags only.

		Time since last harvesting (years)				Sample sizes (number of plots)					
		MAN		UNM		Bats		Birds		Beetles	
	Sites	Mean	SD	Mean	SD	MAN	UNM	MAN	UNM	MAN	UNM
Lowlands	Auberive	7.3	5.8	24.6	12.4	12	12	12	12	12	12
	Bois du Parc	NA	NA	39.0	NA			5	5	5	4
	Chizé	8.6	4.9	26.3	13.0	12	12	12	12	12	12
	Citeaux	9.8	3.9	42.5	7.4	5	5	6	6	6	6
	Combe-Lavaux	3.3	3.3	38.0	0.6			4	4	4	4
	Fontainebleau	6.8	7.3	115.9	29.8	16	13	15	12	13	12
	Haut-Tuileau	4.7	3.8	24.6	5.6	7	7	7	7	7	7
	Rambouillet	6.5	6.2	11.8	4.6	7	8	8	8	8	8
	Verrières	4.5	5.7	51.0	NA	2	3	4	4	4	4
Mountains	Ballons-Comtois	9.8	4.3	26.4	5.1			8	8	8	8
	Engins	NA	NA	100.0	NA					5	5
	Haute Chaine du Jura	10.1	4.7	29.9	11.9			8	8		
	Lure	23.8	17.7	40.3	17.5			4	4	4	4
	Ventron	1.8	1.2	18.8	0.5			4	4	4	4
	Ventoux	39.2	31.8	98.4	46.1			5	5	5	5
Means and totals		8.8	11.5	47.2	39.6	61	60	102	99	97	95

Tableau 19 : Characteristics of the sites used to analyse the response of three taxonomic groups to tree microhabitats in French managed forests (MAN) and in strict forest reserves (unmanaged, UNM). SD: standard deviation; NA: data not available.

Biodiversity censuses and classification

We inventoried bats, birds and saproxylic beetles based on the sampling design described above, but with different data subsets for each taxon (Tableau 19). In particular, for safety reasons, bats were inventoried in lowland forests only. Protocols are detailed in Bouvet et al. (2016) for bat and bird censuses, and *e.g.* Bouget et al. (2014a) for saproxylic beetles. The main elements are summarized in Tableau 20 and Annexe 14.

	Bats	Birds	Saproxylic beetles
Method	Ultrasonic point counts	Point counts (breeding bird survey protocol)	Flight interception traps (Polytrap™)
Periods	April-May, June-July and August-September	April-May and May-June	April-August
Sampling effort	3 censuses 30 min each	2 censuses 5 min each	3 months, 2 traps per plot (except for 2 sites), emptied once a month
Species identification	2 trained chiropterologists per site with Pettersson D980 and D240x detectors and Marantz PMD620 recorder	1 trained ornithologist per site	Trained entomologists and taxonomic group specialists

Tableau 20 : Summary of the biodiversity census protocols. See Annexe 14 for a detailed description.

Species of different taxa were classified consistently according to their conservation status and ecological preferences. For birds and bats, the group "Threatened species" combined critically endangered (CR), vulnerable (VU) and near threatened (NT) species, according to the French national red-list classification (UICN France et al., 2011). In the absence of a French red list for saproxylic beetles, we characterised the degree of geographic rarity for each species according to the species patrimonial values defined in the FRISBEE database by Bouget et al. (2008) for metropolitan France

(http://frisbee.nogent.cemagref.fr/index.php/en/). In this database, commonness and rarity classes are based on geographic range and local abundance (Rabinowitz, 1981), rare species having a wide range but a consistently low abundance (patrimonial value of 3) or a narrow range and possible high local abundance (patrimonial value of 4). Birds and bats were classified into two ecological groups based on habitat specialization: forest specialists and cavity nesters (Bouvet et al., 2016; Dietz et al., 2009; Gregory et al., 2007). Saproxylic beetles were classified into three ecological groups or guilds (shade-tolerant species, cavity dwellers and fungus dwellers) according to the FRISBEE database. Contrary to birds and bats, we were not able to assign levels of forest specialization to saproxylic beetle species since our trait database was devoid of such a characteristic. We therefore used shade-tolerance, based on the canopy cover niche position of saproxylic beetle species described in the trait database. Since many saproxylic beetle species are known to be light-demanding species and to prefer sunny forests (Miklín et al., 2018; Seibold et al., 2015), we were aware that shade-tolerant saproxylic beetles may not be qualified as strict forest specialists comparable to the two other taxa.
We then calculated biodiversity indices at two levels: (i) total species richness (number of species) and abundance; (ii) species richness and abundance per conservation status and ecological group (guild). Since sampling methods differed among the three groups, abundance values were calculated differently: for bats, we summed the number of contacts per species across the sampling season as a proxy for true abundance per species; for birds, since individuals were differentiated in the field, we summed the number of individuals heard or seen across the sampling season; for saproxylic beetles, we summed the number of individuals caught across the sampling season.

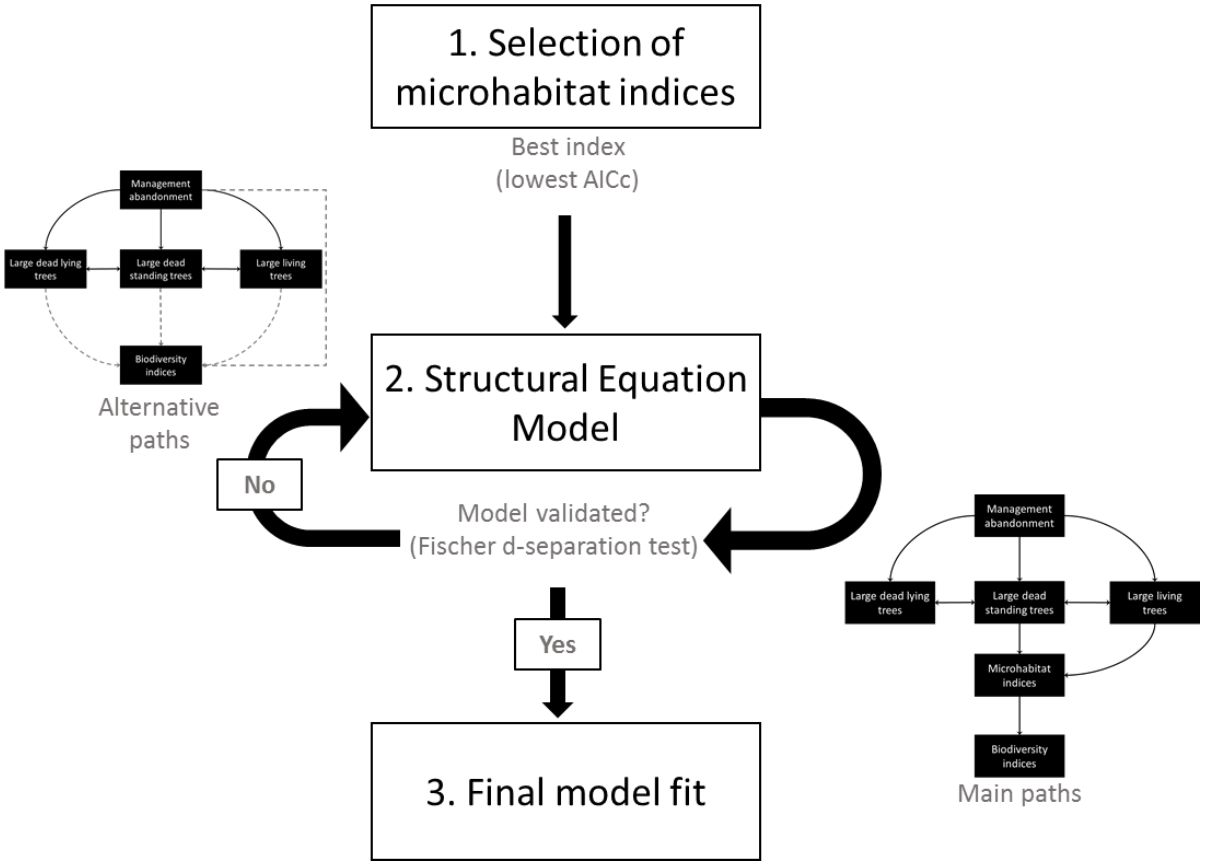


Figure 10 : Data analysis flowchart. We stopped at step 1 only if the null model had the lowest Akaike Information Criterion corrected for small samples (AICc).

Statistical analyses

We processed all the analyses with the R software v. 3.3.2 (R Core Team, 2016). We followed the three-step analysis framework illustrated in Figure 10.

We first fitted single-variable models with biodiversity indices (richness, abundance) as a response variable, and microhabitat indices (densities, diversities and density of cavities, conks of fungi and cracks) as explanatory variables. We used generalized linear mixed models (GLMM) with a Poisson error distribution and log link for richness and abundance, with site as a random effect (the sampling design is one-way nested). We added an observation-level random effect to account for potential overdispersion (Harrison, 2014). All the GLMMs were fitted with the glmer function in the lme4 package (Bates et al., 2015). We compared these models and an additional null model containing only the intercept and the random effects with the Akaike Information Criterion corrected for small samples (AICc, Akaike, 1974). We selected the microhabitat model with the lowest AICc. This provided the most informative microhabitat index with respect to the biodiversity indices analysed. If the null model had the lowest AICc, we stopped the analyses at step 1 (Figure 10). In the other cases, we proceeded to the second step with the microhabitat index selected. Note that models with management abandonment or large structural elements as explanatory variables were also fitted but are presented in supplementary materials only (Annexe 15).

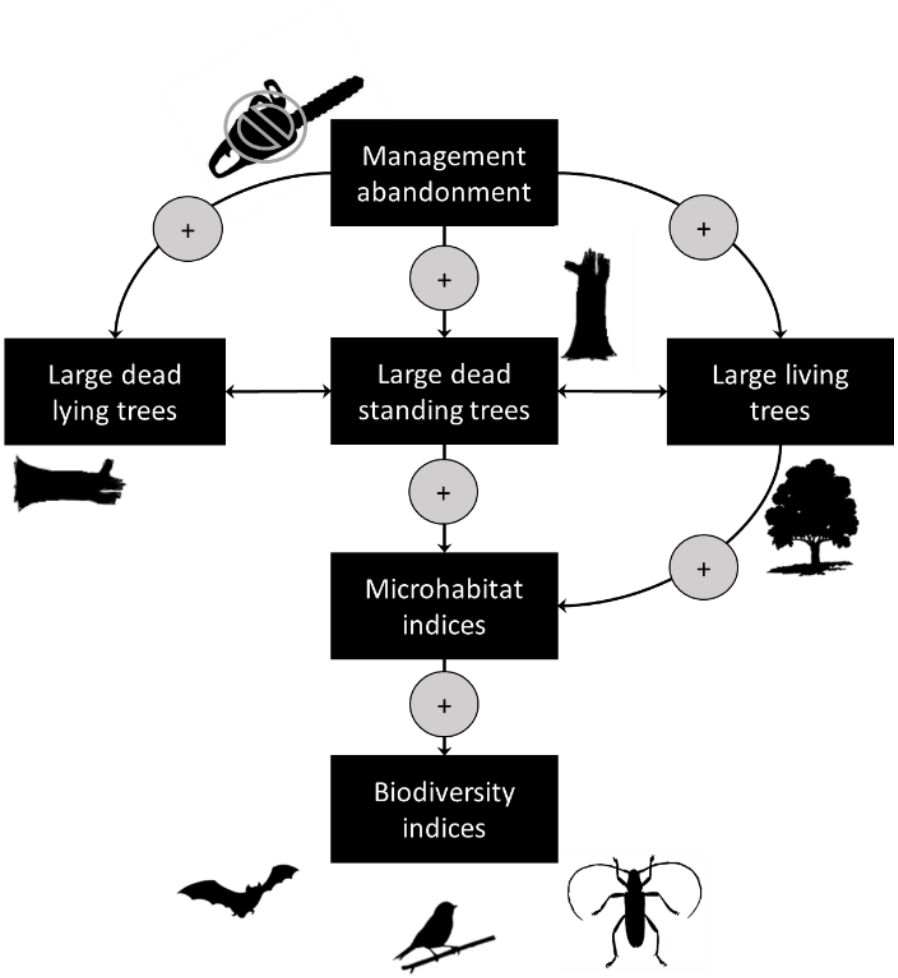


Figure 11 : General path diagram (metamodel) representing the main hypotheses tested. "+" signs in the circles represent the hypothesized direction of the effect. Bidirectional arrows mean correlated errors. Alternative hypotheses (or paths not figured here) involve direct link between large structural elements (large living, large dead standing – snags – or large dead lying trees – logs) or management abandonment and biodiversity indices.

Second, for each biodiversity metric, we used the microhabitat index selected in the previous step to fit a structural equation model (SEM, using the package piecewiseSEM, Lefcheck, 2016, Figure 11). SEMs use dependence directional pathways (Lefcheck, 2016) to confirm hypothesized causal relationships between several variables. SEMs are a generalisation of path analysis that make possible the use of models with different error distributions in the same path (Shipley, 2009). The models were of the same form as mentioned above: when the response variable was a biodiversity index, we fitted GLMMs with a Poisson error distribution, log link and site and observation as random effects; when the response variable was a forest structure variable (either living tree, standing deadwood or microhabitat index), we fitted linear mixed effects models with a Gaussian error distribution, identity link and site as a random effect (function lme, library nlme, Pinheiro et al., 2016). Whenever necessary, correlated errors between explanatory variables were also specified, especially between large structural elements descriptors (Figure 11). We first fitted a SEM with a preferential path that corresponded to our main hypotheses (*i.e.* mediation by microhabitats, Figure 11) and tested for the missing paths with Fisher d-separation tests (Shipley, 2013). When no path involving the final response variable (*i.e.* the biodiversity index) was found significantly missing, we validated the SEM and proceeded to step 3. If a missing path involving the biodiversity index was found significant, we then refitted alternative SEMs until we found the one with the lowest AIC and no significantly missing path. We then proceeded to step 3.

Third, we analysed the significance and magnitude of the relationship between the biodiversity variable and its direct explanatory variables selected in the SEM, as well as the relationships between explanatory variables within the SEM (*i.e.* management, large structural elements and microhabitat indices, Figure 11).

Results

In total, we identified 19 bat species (3242 contacts), 57 bird species (3934 individuals), and 404 saproxylic beetle species (32331 individuals).

Microhabitat index selection

In the first step of our analysis, based on AICc comparison, we selected the microhabitat index that best represented the biodiversity of the different groups analysed. The microhabitat index selected was then injected in structural equation models to confirm whether it had a link with large structural elements and ultimately an effect on biodiversity.

For bats, diversity indices were the most often selected (Tableau 21, see Annexe 15 for extensive results): total microhabitat diversity influenced total and forest specialist richness; microhabitat diversity borne by snags influenced total abundance (all species). Density of microhabitats borne by snags influenced richness of cavity roosters. For richness of red-listed species, the null model was selected, and we did not analyse this group further.

For birds, diversity indices were also the most often selected (Tableau 21, see Annexe 15 for extensive results): total diversity influenced total, forest specialist and cavity nesters richness, as well as total and cavity nester abundances; microhabitat diversity borne by snags influenced red-listed and forest specialist abundances. For richness of red-listed species, the null model was selected, and we did not analyse this group further.

For saproxylic beetles, the results were more heterogeneous (Tableau 21, Annexe 15). Density of microhabitats borne by snags influenced total richness and rare species abundance; cavity density influenced shade-tolerant species richness and cavity and fungi dwellers abundances; density of trees with more than three microhabitat types influenced cavity dwellers richness; crack density influenced

total abundance; and conk density influenced shade-tolerant species abundance. Finally, the null model was selected for rare species and fungi dwellers richness, and we did not analyse these groups further.

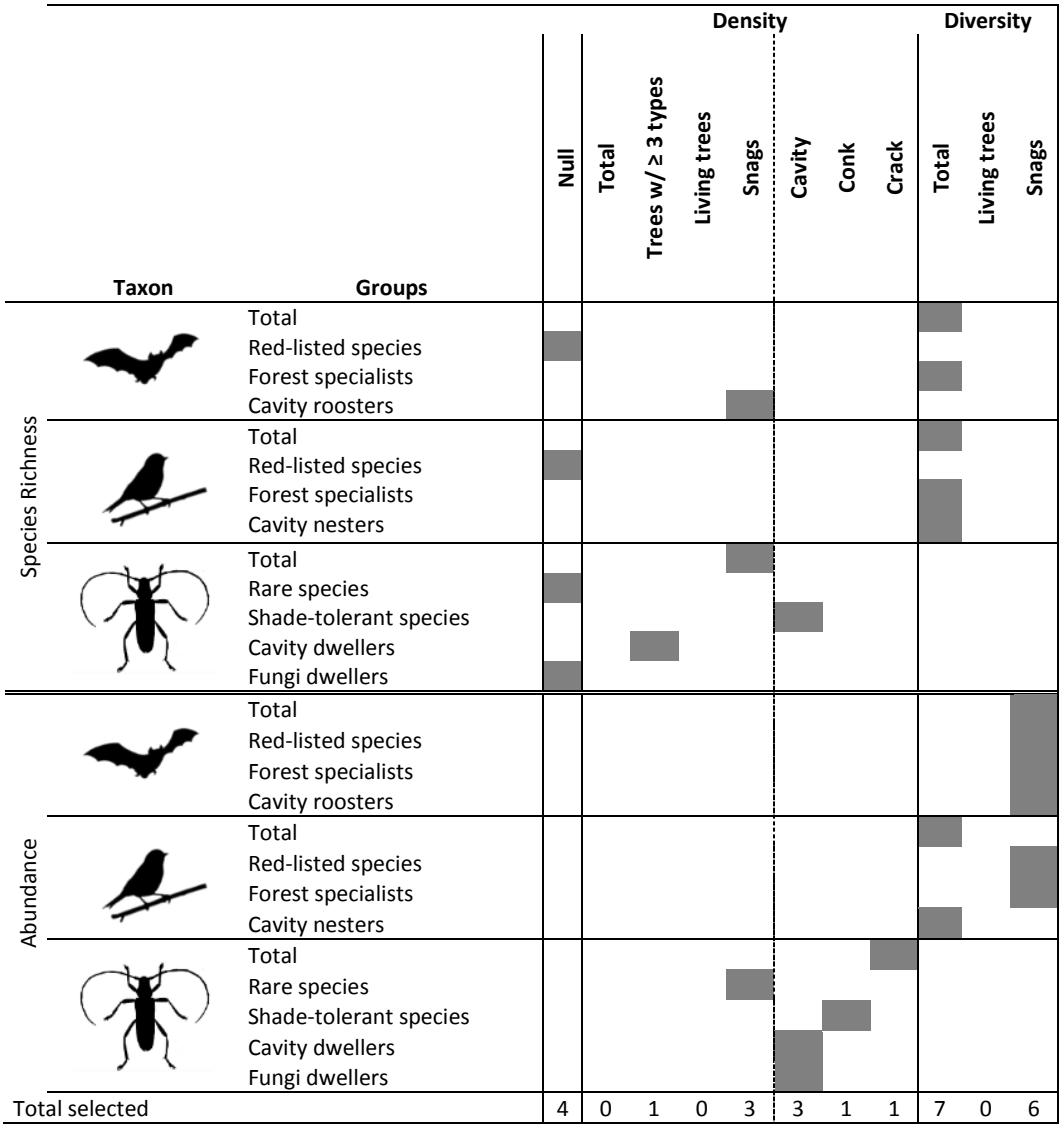


Tableau 21 : Microhabitat metrics selection based on Akaike Index Criterion corrected for small samples (AICc). Grey cells figure models with the lowest AICc. See Annexe 15 for extensive results and AICc values.

To sum-up, based on model selection, out of the ten microhabitat indices we compared across taxa and groups, microhabitat diversity indices were selected thirteen times, microhabitat density indices nine times and the null model four times (Tableau 21). Note that in numerous cases, the AICc of several competing models were comprised within two points, sometimes including the null model but also models with large structural elements or management abandonment as explanatory variables (Annexe 15).

Structural equation models for richness and abundance

In the second step of the analysis, we fitted 22 SEMs (Tableau 22) using microhabitat indices selected during step 1. Out of these SEMs, seventeen were validated without resorting to alternative paths: ten had non-significant Fisher d-separation test ($p>0.05$), and seven significant ($p<0.05$) or marginally significant ($p<0.1$) Fisher d-separation test due to missing links between management, large structural elements and microhabitats, but not involving a missing link with biodiversity. All these model showed a direct link between a microhabitat index and biodiversity (Tableau 22). In the last five cases, the SEMs were not validated (Fisher d-separation test, $p<0.05$) with missing paths involving a biodiversity index as response variable. We refitted these SEMs with alternative paths (Figure 11) and selected the one with the lowest AIC without any significantly missing path: this resulted in SEMs with direct links between biodiversity and (i) management abandonment in three cases, and (ii) large structural elements in two cases (Tableau 22).

	Taxon	Groups	Management abandonment	Large Elements	Microhabitats
Species richness		Total			Diversity **0.17***
		Red-listed species			NA
		Forest specialists			Diversity **0.21(*)**
		Cavity roosters			Density (snags) **0.35***
		Total			Diversity **0.06***
		Red-listed species			NA
		Forest specialists			Diversity **0.08***
		Cavity nesters			Diversity **0.13****
		Total	**-0.09***		
		Rare species			NA
		Shade-tolerant species			Conk density **0.08 (*)**
		Cavity dwellers			Density (trees w/ ≥ 3 types) **0.33(*)**
		Fungi dwellers			NA
Abundance		Total			Diversity (snags) **0.42***
		Red-listed species			Diversity (snags) **0.72***
		Forest specialists			Diversity (snags) **0.61***
		Cavity roosters	**1.06*****		
		Total	**0.11*****		
		Red-listed species			Diversity (snags) **0.11ns**
		Forest specialists			Diversity (snags) **0.10****
		Cavity nesters			Diversity **0.17*****
		Total		Basal area (living trees) **0.13***	
		Rare species			Density (snags) **0.18(*)**
		Shade-tolerant species		Volume (snags) **-0.13***	
		Cavity dwellers			Cavity density **0.28ns**
		Fungi dwellers			Cavity density **0.19****

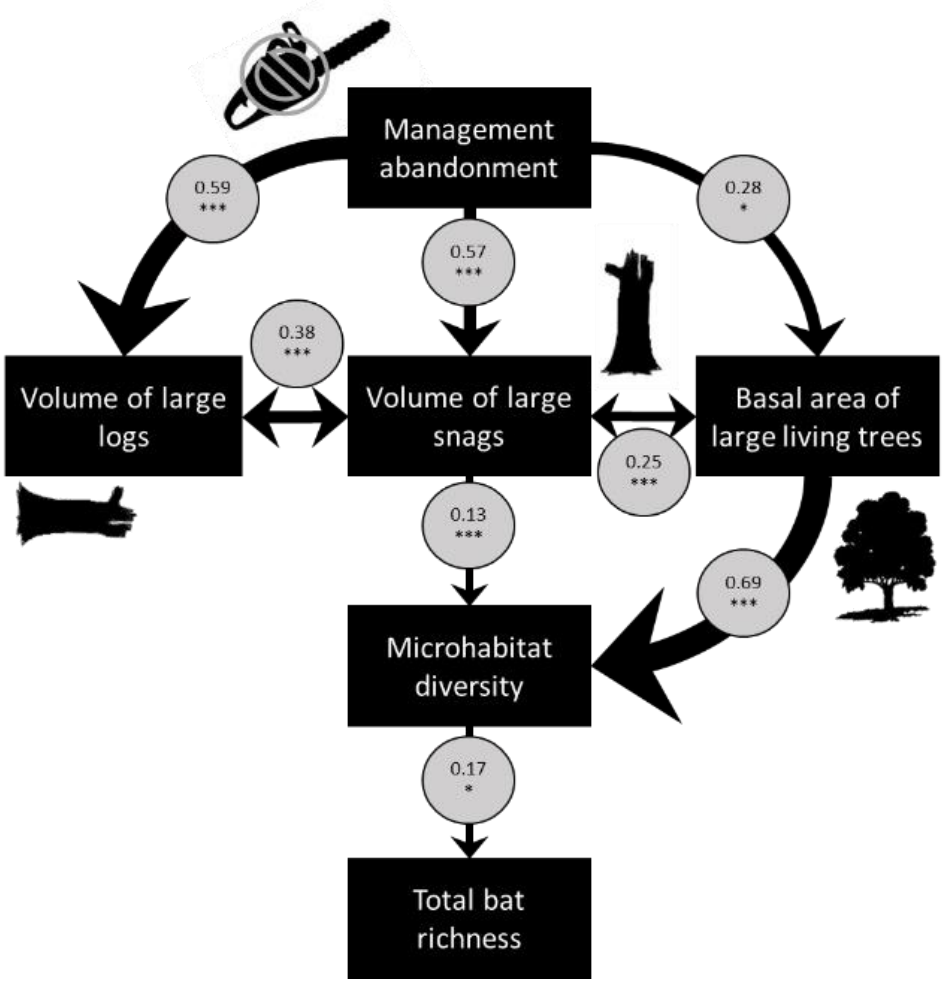
*Tableau 22 : Standardized slope estimates linking biodiversity of bats, birds and saproxylic beetles and explanatory variables. Coefficients in bold are issued from generalized linear mixed models with a Poisson error distribution and site and observation as random effects within a structural equation model (SEM) framework (see Figures 1 and 2). Other coefficients issued from SEMs are presented in Annexe 16. ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result. NA: Process stopped at step 1.(Figure 10).*

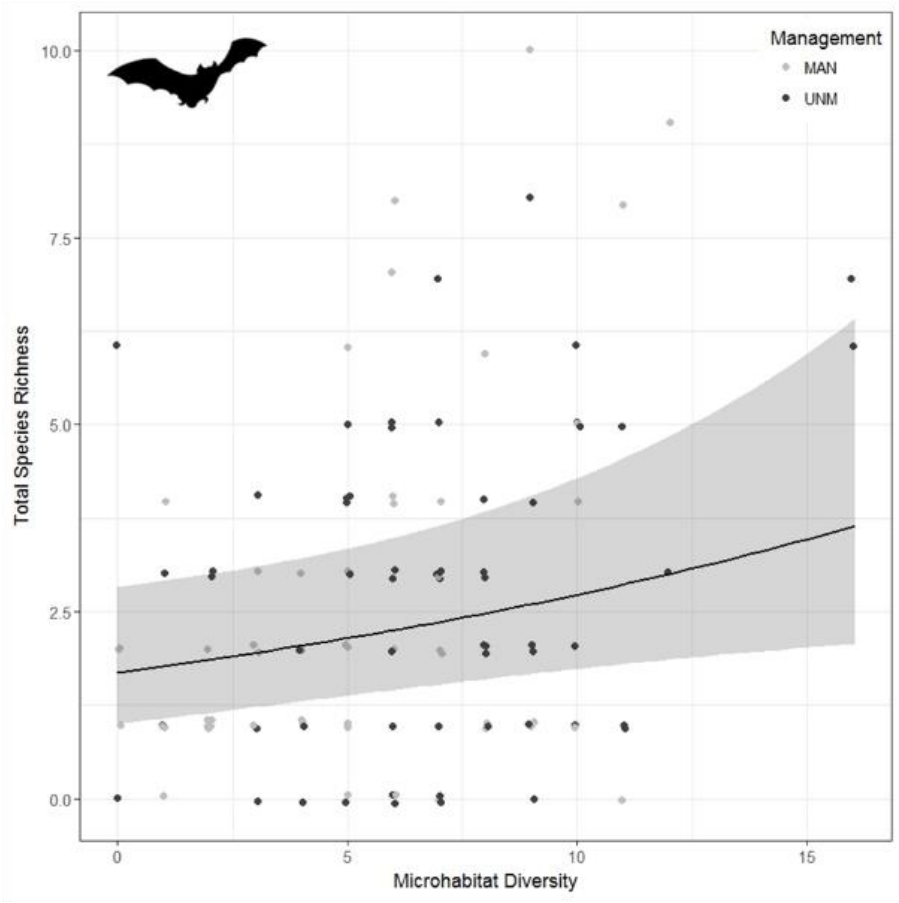
As expected, most relationships between management type, large structural elements and microhabitat indices within each SEM were significant and positive as illustrated in Figure 12 (see Annexe 16 for detailed results). All the significant relationships between biodiversity and microhabitat indices were positive (Tableau 22 and Annexe 16). In terms of magnitude, we observed the strongest

relationships for bat abundances (Tableau 22) and to a lesser extent for bat richness (Figure 12, see also standardized estimates in Annexe 16). For example, an increase from 0 to 5 in the diversity of microhabitat types borne by snags (about half of the possible range of 0-9) resulted in an increase in total bat abundance from 6.8 to 35.5 (multiplied by 5.2). Contrastingly, a comparable increase from 0 to 10 in the total diversity of microhabitat types (about half of a possible range of 0-18) resulted in an increase in total bat richness from 1.7 to only 2.7 species (multiplied by 1.58, Figure 12). Results in magnitude for the other groups were either comparable to bat species richness (for cavity-nesting bird richness, forest specialist and cavity-nesting bird abundances, fungi-dwelling saproxylic beetle abundance, Tableau 22) or smaller (total bird and forest specialist richness, Tableau 22). We observed marginally significant relationships between forest specialist bat richness and microhabitat diversity ($p=0.06$), between shade-tolerant saproxylic beetle richness and conk density ($p=0.06$), cavity-dwelling saproxylic beetle richness and density of trees with more than three microhabitats ($p=0.08$) and between rare saproxylic beetle abundance and density of microhabitats borne by snags ($p=0.06$). Finally, relationship between cavity-dwelling saproxylic beetle abundance and cavity density was non-significant ($p>0.1$).

In the case of alternative SEMs not involving a direct link between biodiversity and microhabitats, we found significant positive relationships between management abandonment and both cavity-roosting bat abundance and total bird abundance ($p<0.001$ in both cases). Conversely, and contrary to our expectations, we found a significant but negative relationship between management abandonment and saproxylic beetle total richness ($p=0.05$). The effect of management abandonment was strongly positive on cavity-roosting bat abundance (three times more in unmanaged forests), moderately positive on total bird abundance, and moderately negative on total saproxylic beetle richness (Tableau 22). Finally, the relationships between total saproxylic beetle abundance and basal area of large living trees and between shade-tolerant saproxylic beetle abundance and large snag volume were significantly negative ($p=0.04$ for both) with a moderate magnitude.

*Figure 12 : Path diagram illustrating the effect of management abandonment (MAN: Managed stands, UNM: Unmanaged stands), large structural elements and tree microhabitat diversity on total species richness of bats. Figures represent the standardised slope estimates resulting from (generalized) linear mixed models (GLMMs). The width of the arrows is proportional to the magnitude of the effect. Bidirectional arrows mean correlated errors. No arrow means no significant effect. On the graph, solid line represents the mean of the model, and grey area the 95% confidence interval. Jittering has been added for visibility. Significance: ***p<0.001, *p<0.05.*





Discussion

A direct link between tree microhabitats and bat and bird biodiversity

Numerous studies have demonstrated the key role of large trees and standing deadwood (snags) for several taxa including birds (*e.g.* Le Roux et al., 2015; Loyn & Kennedy, 2009), bats (*e.g.* Kalcounis-Rüppell et al., 2005; Regnery et al., 2013a) and beetles (*e.g.* Bouget et al., 2014a; Müller et al., 2014). However, it is still unclear whether these large structural elements are a favourable habitat as a whole or if the microhabitats they bear are in fact the significant driver. The same reasoning holds for management abandonment: per se, it can be favourable to biodiversity (Paillet et al., 2010), but it can also favour the development of structural features that support biodiversity (Bouget et al., 2014b; Bouvet et al., 2016; Paillet et al., 2017; Regnery et al., 2013a). These factors are inextricably linked by a causal relationship.

Using causal pathways analysis, we showed that management abandonment indeed favoured large structural elements that are more likely to bear microhabitats (Paillet et al., 2017). In turn, microhabitats often favoured richness and abundance of birds and bats – and to a lesser extent saproxylic beetles – more directly than large structural elements or management abandonment did (see Regnery et al., 2013a for bats and birds in Mediterranean forests). Interestingly, in our study, microhabitat diversity indices explained biodiversity more often than densities, which indicates that habitat quantity seems to be less important than habitat diversity for certain groups of species (*e.g.* Janssen et al., 2017; Redolfi De Zan et al., 2014; Seibold et al., 2016 for saproxylic beetles). Here, microhabitat diversity – rather than density – significantly explained most bat and bird indices (9 out of 16). Remarkably, the links between microhabitat diversity and bat abundances (including total, red-listed and forest species) were the strongest we observed. European birds and bats can use a wide range of microhabitat types (Gregory et al., 2007; Regnery et al., 2013a), and various co-occurring microhabitat types are likely to favour several microhabitat foraging and nesting species, more than the abundance of a given microhabitat type only. For example, cavity dwellers use cavities for nesting/roosting but also feed on crown deadwood or on other resources identified as microhabitats in our study (*e.g.* ivy or bryophytes). In addition, softened and dried wood, with the presence of conks of fungi, decaying bark and cracks, allows cavity builders – and more generally saproxylic species – to reproduce and forage more easily (*e.g.* Jackson & Jackson, 2004). These examples show the complementarity between various microhabitat types, which is likely to explain why diversity indices better explained biodiversity patterns of birds and bats in our study. Our results also support the habitat-heterogeneity hypothesis (Tews et al., 2004), which postulates that the more the niches available, the higher the number of species.

Inconclusive links between tree microhabitats and other groups

The link between microhabitats and saproxylic beetles was less systematic or significant. Other factors beyond the scope of this study, in particular total deadwood volume or diversity, seem to play a greater role; this has been thoroughly demonstrated elsewhere (*e.g.* Bouget et al., 2014a; Lassauce et al., 2011; Müller & Bütler, 2010). The absence of correlation could also be an effect of the scale at which we sampled microhabitats. Using a rapid habitat assessment that included microhabitats on a sampling design partially overlapping ours, Bouget et al. (2014a) showed that, at a 1-ha scale, the density of cavity- or fungus-bearing trees significantly influenced both richness and composition of saproxylic beetle communities. This relationship does not seem to hold – or is less detectable – over a smaller area (we inventoried microhabitats over ca. 0.12 ha). Variability of this relationship due to biogeographic conditions may have also affected our results (see Lassauce et al., 2011 for variation of the relationship between saproxylic organisms and deadwood volume). However, in our case, exploratory analyses did not reveal interactions between geographic factors (*e.g.* elevation) and our explanatory variables.

With the remarkable exception of red-listed bat abundance, the biodiversity indices of the other rare or red-listed species in our study were poorly explained by microhabitat metrics (nor were they explained by large structural elements or management abandonment). This means that the drivers for these species are still to be found (but see also methodological limitations below). Finally, only cavity bat and total bird abundances as well as total saproxylic beetle richness were significantly explained by management abandonment. For birds and bats, management abandonment in forest reserves may provide favourable habitats but also low levels of human disturbance (Bouvet et al., 2016). Compared to previous results (Paillet et al., 2010), the negative result for saproxylic beetles is more surprising, but may be due to the fact that most of the reserves we studied are relatively young and display relatively small amounts of favourable habitats and features compared to other European references (Bouget et al., 2014b; Paillet et al., 2015b). As a consequence, stands may still be in an accumulation phase where light conditions are probably not diverse enough to favour both forest specialists and light-demanding species at a small scale (see *e.g.* Bouget et al., 2014a; Seibold et al., 2016 for saproxylic beetles) and the potential effect of microhabitats or large structural elements may be masked by such unfavourable light conditions (Miklín et al., 2018). It is thus important to take the temporal dimension of this result into account and we may expect biodiversity to increase when the reserves would be mature enough to show spatial horizontal heterogeneity at the stand scale (Paillet et al., 2015b).

Methodological limitations

The sampling methods we used are intrinsically imperfect ways to assess biodiversity. Sampling methods based on point counts or flight-traps tend to be biased towards the most active, noisy or abundant species (*e.g. Pipistrellus pipistrellus*, *Fringilla coelebs*, or *Scolytinae* in general) while less detectable species that potentially depend on microhabitats may be underestimated (*e.g.* woodpeckers). For example, microhabitat-associated beetles are difficult to catch using window-flight traps only, compared with emergence traps directly installed on the microhabitats (Gouix & Brustel, 2012). However, window-flight traps provide higher yields and probably better estimates of species richness and abundance, while other sampling methods are probably more difficult to standardize. In addition, microhabitat inventories are subjected to observer effects and imperfect detectability (Paillet et al., 2015a) which may blur the estimates of diversity and density. The typology we used might also be too coarse for some specific taxa: for example, we did not differentiate between cavity types (*e.g.* with or without mould) that could support very different species assemblages. Yet, progresses towards more specific and exhaustive inventories have recently been done (Larrieu et al., 2018), but assessing the species dependence on rare microhabitat types now require larger datasets to be powerful enough for statistical analyses. Altogether, these biases, some of which can be observed for other forest structure measurements (see discussion in Paillet et al., 2015a), partly explain the relatively low levels of correlation we observed in this study.

Conclusions

Does this study validate tree microhabitats as biodiversity indicators?

In their recent review, Gao et al. (2015) emphasized the need for more studies on potential biodiversity indicators which currently show moderate evidence (*i.e.* few studies but with coherent results), including tree microhabitats. First, we showed that, based on our framework, microhabitat diversity was a more direct predictor of biodiversity than large structural elements of forest structure. Therefore, microhabitat diversity tends to mediate the effects of large elements on biodiversity, especially for birds and bats. This result also emphasizes the importance of the metrics (*e.g.* quantity vs diversity) used in the definition of biodiversity indicators. Indeed, even though ecological theory and management recommendations stress the importance of habitat diversity as well as quantity, it is surprising that most of the indicators used for national and international reporting are abundance metrics (*e.g.* deadwood volume is used by Forest Europe and the European Environment Agency as an

indicator of biodiversity for their various reports). Here, we showed that microhabitat indicators based on diversity metrics may perform better than those based on abundance, although they may be harder to interpret (Brin et al., 2009; Noss, 1990) and to implement in daily management. In any case, they are worth considering when validating structure-based biodiversity indicators.

Second, we showed that microhabitats generally mediate the causal link between management abandonment, abundance of large structural elements and biodiversity for several groups and taxa. However, the magnitude of the correlations between microhabitat and biodiversity indices remained moderate, except for bat abundances. To our knowledge, no strict magnitude threshold has been defined to validate a proxy as a biodiversity indicator. Niemela (2000) states that the correlation should be significant and strong, without further precision on the magnitude, but large-scale analyses of biodiversity rarely provide strong correlations since most of the variations observed are generally due to uncontrolled variations (*e.g.* due to climate, phenology or sampling). In addition, several indirect biodiversity indicators routinely used in forest monitoring also show rather weak magnitudes of correlations (see Lassauce et al. (2011) for deadwood volume and saproxylic organisms and Gao et al. (2015) for a broader view). In our study, microhabitat indices tended to correlate significantly with abundance and richness indices, but showed low levels of magnitude. Since most of the knowledge accumulated to date on microhabitats concerns individual species or small groups (Larrieu et al., 2018), broader evidence is probably still needed at the community level to confirm these results.

Implications for forest monitoring and management

Microhabitats seem to play a complementary role with other potential biodiversity indicators, including those tested here (large living trees, snags and logs). They also seem to have a more direct – and functionally relevant – role than large structural elements. As suggested by Larrieu et al. (2018), our results confirm that it would be interesting to add microhabitat censuses to forest inventories or daily forest management operations as a complementary biodiversity indicator. In addition, it would be interesting to use causal models to generalize this approach to other potential indicators (*e.g.* tree diversity, forest fragmentation… Forest Europe, 2015b) and to assess their respective role in a robust, correlative and causal way. It would also be informative to assess the relevance of modular, additive indicators, combining several individual metrics related to microhabitats, deadwood and large trees; however, such composite indicators still need to be defined and tested. Another perspective would be to test the relation between microhabitats and different taxa like hoverflies, moths, amphibians or mammals (see *e.g.* Larrieu et al., 2015; Piraccini et al., 2017; Rowland et al., 2017). This would require large scale monitoring including, among other variables, microhabitats observation and multi-taxon inventories (Zellweger et al., 2015).

In terms of practical forest management, we showed that favouring the diversity of microhabitats through the conservation of large structural elements generally benefits the biodiversity of bats and birds. Yet, thresholds for optimal biodiversity conservation in managed forests remain to be empirically demonstrated, politically accepted and ultimately implemented by managers. Increasing heterogeneity of forest stands tends to increase the biodiversity of some groups as demonstrated here. However, in our case, the response to the increase in microhabitat diversity was not systematic, especially for species at stake, like red-listed species, for which specific measures have to be taken.

Acknowledgements

We are indebted to the many chiropterologists, ornithologists and entomologists involved in the project. Without their implication, no data would have been available for this research. We thank T. Barnouin (ONF), D. Barré (ONF), I. Bassi (ONF), J. Bernard (ONF), S. Coulette (RNN Ballons Comtois), T. Darnis (ONF), P. Denis (ONF), B. Devaux (ONF), C. Druesne (RNN Ventron), B. Fauvel (ONF), T. Freund

(ONF), V. Godreau (ONF), J. L'Huillier (ONF), F. Malgouyres (ONF), C. Marck (ONF), P. Millarakis (ONF), C. Moliard (Irstea), T. Noblecourt (ONF), B. Nusillard (Irstea) A. Perthuis (ONF), J. Rosset (RNN Haute Chaine du Jura), F. Soldati (ONF), L. Tillon (ONF) and R. Truckenwald (ONF). We are grateful to J-J. Boutteaux (ONF), B. Fritsch (RN Bois du Parc), R. Lecomte (RN Chalmessin), L. Servières (RN Combe-Lavaux) for organizing field work. We also thank I. Piney and M. Baltzinger for chainsaw and other iconographic suggestions; G. Percel and F. Laroche for constructive discussions and careful reading. V. Moore significantly polished the language of this paper. Two anonymous reviewers' suggestions helped improving a previous version the manuscript. This research was funded by the French Ministry in charge of Ecology (Convention Cemagref-DEB (MEEDDAT), Action GNB; the program "Biodiversité, Gestion Forestière et Politiques Publiques" (BGF), convention GNB 10-MBGD-BGF-1-CVS-092, no CHORUS 2100 214 651; and Convention DEB-Irstea, Action GNB-valo) and the Office National des Forêts (Convention ONF-Cemagref, Action 5, 2008).

Authors' contributions

Y.P., O. G. and F.G. conceived the ideas and designed the methodology; Y.P., F.A., C.B., V.B. and N.D. contributed to and organized data collection; Y.P. and S.d.P. analysed the data; Y.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data available via Dryad Digital Repository https://doi:10.5061/dryad.101p50d (Paillet et al., 2018).

References

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transaction on Automatic Control*, **19**, 716-23.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1-48.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The FRench Information system on Saproxylic BEetle Ecology (FRISBEE): An ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie (La Terre et la Vie)*, **63**, 33-36.

Bouget, C., Larrieu, L. & Brin, A. (2014a) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, **36**, 656-64.

Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L. & Gosselin, F. (2014b) Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Animal Conservation*, **17**, 342-53.

Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O. & Gosselin, F. (2016) Effects of forest structure, management and landscape on bird and bat communities. *Environmental Conservation*, 1-13.

Brin, A., Brustel, H. & Jactel, H. (2009) Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in Maritime pine plantations. *Annals of Forest Science*, **66**, 306.

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.C. & Watson, R. (2010) Global biodiversity: Indicators of recent declines. *Science*, **328**, 1164-68.

Bütler, R., Lachat, T., Larrieu, L. & Paillet, Y. (2013). Habitat trees: key elements for forest biodiversity. In *Integrative approaches as an opportunity fir the conservation of forest biodiversity* (eds D. Kraus & F. Krumm), pp. 84-91. European Forest Institute, Freiburg, DEU.

Chirici, G., McRoberts, R.E., Winter, S., Bertini, R., Bröändli, U.B., Asensio, I.A., Bastrup-Birk, A., Rondeux, J., Barsoum, N. & Marchetti, M. (2012) National forest inventory contributions to forest biodiversity monitoring. *Forest Science*, **58**, 257-68.

Dietz, C., Von Helversen, O. & Nill, D. (2009) *L'encyclopédie des chauves-souris d'Europe et d'Afrique du Nord : Biologie, caractéristiques, protection* Delachaux et Niestlé, Paris.

Forest Europe. (2015a). State of Europe's Forests 2015. In.

Forest Europe. (2015b). The updated pan-european indicators for sustainable forest management. In (ed Ministerial Conference on the Protection of Forests in Europe), Zvolen, Slovak Republic.

Gao, T., Nielsen, A.B. & Hedblom, M. (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, **57**, 420-34.

Gouix, N. & Brustel, H. (2012) Emergence trap, a new method to survey Limoniscus violaceus (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation*, **21**, 421-36.

Gregory, R.D., Vorisek, P., Van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. & Burfield, I.J. (2007) Population trends of widespread woodland birds in Europe. *Ibis*, **149**, 78-97.

Harrison, X.A. (2014) Using observation-level randomeffects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2014**.

Jackson, J.A. & Jackson, B.J.S. (2004) Ecological relationships between fungi and woodpecker cavity sites. *Condor*, **106**, 37-49.

Janssen, P., Fuhr, M., Cateau, E., Nusillard, B. & Bouget, C. (2017) Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, **205**, 1-10.

Kalcounis-Rüppell, M.C., Psyllakis, J.M. & Brigham, R.M. (2005) Tree roost selection by bats: An empirical synthesis using meta-analysis. *Wildlife Society Bulletin*, **33**, 1123-32.

Larrieu, L. & Cabanettes, A. (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Canadian Journal of Forest Research*, **42**, 1433-45.

Larrieu, L., Cabanettes, A. & Sarthou, J.P. (2015) Hoverfly (Diptera: Syrphidae) richness and abundance vary with forest stand heterogeneity: Preliminary evidence from a montane beech fir forest. *European Journal of Entomology*, **112**, 755-69.

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B. & Vandekerkhove, K. (2018) Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecological Indicators*, **84**, 194-207.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **11**, 1027-39.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015) Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation*, **191**, 558-66.

Lefcheck, J.S. (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573-79.

Lindenmayer, D.B. & Likens, G.E. (2010) The science and application of ecological monitoring. *Biological Conservation*, **143**, 1317-28.

Loyn, R.H. & Kennedy, S.J. (2009) Designing old forest for the future: Old trees as habitat for birds in forests of Mountain Ash Eucalyptus regnans. *Forest Ecology and Management*, **258**, 504-15.

Miklín, J., Sebek, P., Hauck, D., Konvicka, O. & Cizek, L. (2018) Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles. *Diversity and Distributions*, **24**, 208-18.

Müller, J. & Bütler, R. (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, 981-92.

Müller, J., Jarzabek-Müller, A., Bussler, H. & Gossner, M.M. (2014) Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation*, **17**, 154-62.

Niemela, J. (2000) Biodiversity monitoring for decision-making. *Annales Zoologici Fennici*, **37**, 307-17.

Noss, R.F. (1990) Indicators for monitoring biodiversity - A hierarchical approach. *Conservation Biology*, **4**, 355-64.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F. & Guilbert, E. (2017) Snags and large trees drive higher tree microhabitat densities in strict forest reserves. *Forest Ecology and Management*, **389**, 176-86.

Paillet, Y., Archaux, F., Du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F. & Guilbert, E. (2018). *Data from: The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles.* Dryad Digital Repository. https://doi:10.5061/dryad.101p50d.

Paillet, Y., Bergès, L., Hjälten, J., Odor, P., Avon, C., Bernhardt-Romermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010) Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conservation Biology*, **24**, 101-12.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F. & Gosselin, F. (2015a) Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. *Ecological Indicators*, **49**, 14-23.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O. & Gosselin, F. (2015b) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management*, **346**, 51-64.

Parviainen, J. & Frank, G. (2003) Protected forests in Europe approaches-harmonising the definitions for international comparison and forest policy making. *Journal of Environmental Management*, **67**, 27-36.

Pierson, J.C., Barton, P.S., Lane, P.W. & Lindenmayer, D.B. (2015) Can habitat surrogates predict the response of target species to landscape change? *Biological Conservation*, **184**, 1-10.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D. & the R Development Core Team. (2016) nlme: Linear and Nonlinear Mixed Effects Models. *R package version 3.1-128*.

Piraccini, R., Cammarano, M., Costa, A., Basile, M., Posillico, M., Boitani, L., Bascietto, M., Matteucci, G., De Cinti, B. & Romano, A. (2017) Habitat trees and salamanders: Conservation and management implications in temperate forests. *Forest Ecology and Management*, **384**, 17-25.

R Core Team. (2016). *R: A language and environment for statistical computing.* 3.3.2. R Foundation for Statistical Computing, Vienna, Austria.

Rabinowitz, D. (1981). Seven forms of rarity. In *The biological aspects of rare plants conservation* (ed H. Synge), pp. 205-17. Wiley, New York.

Redolfi De Zan, L., Bellotti, F., D'Amato, D. & Carpaneto, G.M. (2014) Saproxylic beetles in three relict beech forests of central Italy: Analysis of environmental parameters and implications for forest management. *Forest Ecology and Management*, **328**, 229-44.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F. & Kerbiriou, C. (2013a) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecological Indicators*, **34**, 221-30.

Regnery, B., Paillet, Y., Couvet, D. & Kerbiriou, C. (2013b) Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? *Forest Ecology and Management*, **295**, 118-25.

Rowland, J.A., Briscoe, N.J. & Handasyde, K.A. (2017) Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-management of arboreal marsupials. *Biological Conservation*, **209**, 341-48.

Scholes, R.J., Walters, M., Turak, E., Saarenmaa, H., Heip, C.H.R., Tuama, É.Ó., Faith, D.P., Mooney, H.A., Ferrier, S., Jongman, R.H.G., Harrison, I.J., Yahara, T., Pereira, H.M., Larigauderie, A. & Geller, G. (2012) Building a global observing system for biodiversity. *Current Opinion in Environmental Sustainability*, **4**, 139-46.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J. & Baraloto, C. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, **53**, 934-43.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Muller, J. (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, **29**, 382-90.

Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**, 363-68.

Shipley, B. (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology*, **94**, 560-64.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305-08.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, **31**, 79-92.

Tillon, L., Bresso, K. & Aulagnier, S. (2016) Tree selection by roosting bats in a European temperate lowland sub-Atlantic forest. *Mammalia*, **80**, 271-79.

UICN France, MNHN, LPO, SOEF & ONCFS. (2011). La liste rouge des espèces menacées en France. In, Paris, France.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde, P. (2009) When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *Forest Ecology and Management*, **258**, 425-35.

Vuidot, A., Paillet, Y., Archaux, F. & Gosselin, F. (2011) Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, **144**, 441-50.

Zellweger, F., Braunisch, V., Morsdorf, F., Baltensweiler, A., Abegg, M., Roth, T., Bugmann, H. & Bollmann, K. (2015) Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests. *Forest Ecology and Management*, **349**, 36-44.

Chapitre 5 - Discussion générale

5.1. A-t-on validé les microhabitats comme indicateur de biodiversité ?

5.1.1 Synthèse des principaux résultats

5.1.1.1 Etablir des standards et quantifier les biais potentiels

La standardisation des procédures assure la qualité des données, mais un transfert vers les utilisateurs finaux n'est pas toujours effectif ou adapté aux exigences d'un travail de gestion en routine. Ainsi, depuis la publication dans les années 2000 des premières listes de microhabitats destinées à leur détermination sur le terrain (*e.g.* Bruciamacchie, 2005; Winter & Möller, 2008), les efforts de définition et d'homogénéisation étaient restés vains. Dans l'article de Larrieu et al. (2018), nous avons proposé une typologie hiérarchique destinée à standardiser les inventaires de microhabitats dans les forêts tempérées et méditerranéennes d'Europe. La nature hiérarchique de cette typologie, au travers de la distinction de formes, de groupes et de types de microhabitats (Tableau 5), permet son utilisation à différents grains de précision et dans différents contextes : opérations de gestion courante, relevés d'inventaire ou suivis scientifiques. En l'absence d'un corpus de connaissance exhaustif sur la biodiversité associée aux microhabitats, cette approche morphologique basée en partie sur les exigences connues des espèces se veut résolument pragmatique. Ainsi, la majorité des seuils qui permettent de savoir à partir de quelles dimensions les microhabitats doivent être relevés a été définie de manière opérationnelle. Cet effort vient compléter les travaux réalisés depuis 2013 par l'Institut Forestier Européen qui a traduit une première version de cette liste en 13 langues (http://www.integrateplus.org/media-center/project-documents.html). Enfin, au-delà de la standardisation des relevés, cet article regroupe une première synthèse bibliographique qualitative sur le lien entre microhabitats et biodiversité (Annexe 1), qui pourra servir de point de départ à d'autres travaux plus complets.

Dans toute démarche qualité, l'établissement de standards s'accompagne d'une quantification des biais qui peuvent affecter des mesures protocolées. Le biais lié à l'observateur est une source connue pour affecter les données issues d'observation (Ahrends et al., 2011; Larjavaara & Muller-Landau, 2013). Dans le cas des microhabitats (Paillet et al., 2015a), nous avons quantifié les effets des observateurs, de leur expérience, du temps passé et de leur familiarité avec ce type d'inventaire. Les résultats de ce test valident en partie nos hypothèses : l'identité de l'observateur a un effet fort sur la détermination des microhabitats sur le terrain ; par contre, l'expérience ou la familiarité avec le protocole ont des effets limités, et dans des sens parfois contraires à ceux attendus (*e.g.* effet négatif de l'expérience sur le nombre de microhabitats par arbre) ; le temps d'inventaire n'a lui pas d'effet. Ces résultats montrent que les relevés de microhabitats sont particulièrement sensibles à l'effet observateur, mais dans des proportions comparables à celles observées pour d'autres types de relevés : inventaires d'oiseaux (Pacifici et al., 2008), d'espèces forestières ligneuses (Chen et al., 2009) ou relevés de hauteurs d'arbre (Larjavaara & Muller-Landau, 2013). Réalisé par des personnes avec des compétences forestières variées, les résultats de ce test questionnent la réputation des microhabitats à être relevés par des observateurs non experts (Regnery et al., 2013b). Il parait ainsi nécessaire de contrôler au maximum ces effets lors des campagnes d'inventaires en appliquant les solutions que nous avons proposées dans l'article (formation des observateurs, utilisation de jumelles, relevés en binôme…). Dans tous les cas, il y a un équilibre à trouver entre la faisabilité des relevés et leur précision, notamment lorsque les grains les plus grossiers de la typologie sont utilisés (Larrieu et al., 2018).

5.1.1.2 Comprendre les facteurs d'influence

La compréhension des facteurs qui affectent les microhabitats est un prérequis indispensable à leur utilisation pratique. En effet, la sensibilité des indices à certains facteurs anthropiques et abiotiques est un préalable à l'évaluation de la robustesse de leur lien avec la biodiversité, mais aussi à leur

utilisation par les gestionnaires dans des contextes précis. Au travers d'analyses à deux échelles, nous avons quantifié l'influence de ces facteurs sur différents indices de microhabitats.

A l'échelle de l'arbre (Paillet et al., preprint), nous avons confirmé les relations entre caractéristiques de l'arbre et microhabitats observées précédemment sur des cas d'étude plus locaux (Großmann et al., 2018; Larrieu & Cabanettes, 2012; Vuidot et al., 2011; Winter et al., 2015) : le nombre et l'occurrence de la plupart des microhabitats augmentent avec le diamètre de l'arbre et sont plus élevés sur arbres morts que sur arbres vivants. Par contre, malgré des dynamiques différentes sur résineux que sur feuillus (Larrieu et al., 2014a), nous n'avons pas validé l'hypothèse d'une accumulation variable en fonction de l'essence d'arbre. Nous n'avons pas non plus montré d'influence forte des conditions abiotiques sur les taux d'accumulation, mais le test rigoureux de cette hypothèse sur les espèces pour lesquelles cela était possible (hêtre, pins) n'a pas été entrepris ici faute de temps.

A l'échelle de la parcelle forestière (Paillet et al., 2017), nous avons partiellement confirmé que l'abandon d'exploitation lié à la mise en réserve intégrale favorisait les microhabitats (densité totale et densités de la plupart des types). En effet, les densités étaient supérieures en réserve de montagne, alors qu'en plaine les différences entre forêts exploitées et non exploitées n'étaient pas statistiquement significatives. Conformément à nos hypothèses, ces différences sont principalement liées aux très gros arbres et aux arbres morts qui, malgré leur contribution marginale à la densité totale de microhabitats, sont les éléments qui font la différence entre forêts exploitées et non exploitées. Enfin, les densités de microhabitats tendent à augmenter avec le temps écoulé depuis la dernière exploitation forestière, même si cette augmentation reste lente (*e.g.* +19% en 50 ans tous microhabitats confondus).

Ces travaux au niveau de la parcelle forestière confirment donc l'importance des arbres morts et des gros arbres pour les microhabitats, qui était déjà mise en évidence par l'analyse au niveau de l'arbre. L'absence de l'effet de l'essence sur l'accumulation de microhabitats avec le diamètre de l'arbre et des effets limités des conditions abiotiques suggèrent que les mécanismes biologiques ou physiques à l'origine de la formation des microhabitats sont relativement homogènes à l'échelle de l'arbre. Ainsi, malgré des niveaux absolus différents en fonction des essences (*e.g.* Vuidot et al., 2011), une augmentation de diamètre ou la sénescence semblent avoir des effets sur les microhabitats relativement similaires, quelles que soient l'essence d'arbre ou les conditions abiotiques. Par contre, le mode de gestion forestière (mise en réserve intégrale) et l'altitude ont des effets assez marqués au niveau de la parcelle forestière, en termes de densités de microhabitats (plus de microhabitats en réserve et en montagne). Ces différences résultent vraisemblablement de facteurs anthropiques liés à un historique de gestion différent entre plaines et montagnes, et qui semblent avoir un effet prépondérant sur celui des conditions abiotiques. En d'autres termes, il est possible qu'une gestion plus extensive en montagne qu'en plaine, ainsi que des conditions d'exploitation plus difficiles, soient les facteurs prépondérants des différences observées en termes de densités de microhabitats. Les facteurs climatiques n'interviendraient que secondairement.

Enfin, les analyses à l'échelle de la parcelle permettent d'établir de premières valeurs de référence pour une gestion forestière en faveur de la biodiversité reposant sur les microhabitats. La quantification des niveaux observables en l'absence de gestion, de la dynamique liée à cet abandon et à l'accroissement du diamètre des arbres sont autant de guides pour les gestionnaires, qui peuvent ainsi s'inspirer de ces données dans leur gestion courante. Ces références sont contextualisées en fonction de l'altitude mais mériteraient des études plus approfondies, notamment en termes de magnitude, dans des contextes plus variés.

5.1.1.3 Mettre en évidence le lien entre indicateur et biodiversité

La majorité des études concernant la biodiversité inféodée aux microhabitats relève de l'observation empirique de certains types de microhabitats et d'expertise naturaliste (Larrieu et al., 2018, Annexe

1). Les approches plus récentes ont cherché à comprendre comment des combinaisons de plusieurs types de microhabitats permettaient d'expliquer des variations de biodiversité. Ces études ont principalement concerné, en Europe, les coléoptères saproxyliques (Bouget et al., 2014; Bouget et al., 2013; Winter & Möller, 2008), les chauves-souris et les oiseaux (Rendigs et al., 2003; Tillon & Aulagnier, 2014) ou les syrphes (Herrault et al., 2016; Larrieu et al., 2015). D'autre part, la performance respective de différents indicateurs de biodiversité (*e.g.* bois mort vs microhabitats) relativement aux mêmes groupes d'espèces a rarement été analysée (Gao et al., 2015). Dans ce contexte, nous avons étudié la réponse de trois groupes taxonomiques (chauves-souris, oiseaux, coléoptères saproxyliques) à différents indices de microhabitats (Paillet et al., in press). L'originalité de cette approche a été d'inscrire cette analyse dans un cadre formel utilisant des modèles à équations structurelles. Cela a permis de confirmer la relation positive entre abandon de l'exploitation forestière (mise en réserve intégrale), quantités de structures forestières de grandes dimensions (arbres vivants, arbres morts debout et au sol, Paillet et al., 2015b) et microhabitats (Paillet et al., 2017). Nous avons validé l'hypothèse selon laquelle l'augmentation de la diversité (plus que de la quantité) de microhabitats avait une influence positive sur la biodiversité des chauves-souris et des oiseaux, et dans une moindre mesure sur les coléoptères saproxyliques. Les microhabitats apparaissent ainsi comme des médiateurs de l'effet de l'exploitation et des structures de grandes dimensions sur la biodiversité. Cependant, la magnitude des effets de la diversité en microhabitats sur la richesse et l'abondance des chauves-souris et des oiseaux reste relativement modeste : par exemple, la richesse en chauves-souris est multipliée par 1.58 pour une augmentation de diversité en microhabitats couvrant la moitié du gradient possible. Ainsi, l'applicabilité pratique des mesures en faveur des microhabitats doit être discutée en fonction des objectifs locaux des gestionnaires, car tous les niveaux de diversité en microhabitats ne sont pas forcément compatibles avec la gestion courante (voir Bouvet et al., 2016 pour un exemple équivalent sur le bois mort).

Résumé des principaux résultats

Etablissement d'une typologie de référence pour les forêts tempérées et Méditerranéennes d'Europe.

Quantifiation de l'effet observateur sur les relevés de microhabitats.

Confirmation de l'influence du diamètre et de la vitalité des arbres sur le nombre et l'occurrence des microhabitats, avec des différences limitées entre essences.

Effet positif de l'abandon d'exploitation par la mise en réserve forestière sur les densités de microhabitats.

Médiation par les microhabitats de l'effet de l'abandon de gestion et des éléments de grandes dimensions (gros arbres vivants et morts, debouts et au sol) sur les chauves-souris et les oiseaux.

5.1.2 Limites méthodologiques

5.1.2.1 Quelle échelle ?

Le problème de la taille de relevé reflétant le mieux les variations de la variable observée n'est pas nouveau et ne trouve pas de réponse unique (*e.g.* Lombardi et al., 2015). Dans le cas des microhabitats et de leur lien avec la biodiversité, la question de l'échelle se pose à double titre : (i) les microhabitats sont relevés sur une petite surface d'environ 0.12ha comparable par exemple à celle utilisée en routine par les inventaires forestiers nationaux (Tomppo et al., 2010) ; (ii) les relevés de biodiversité sont effectués sur des surfaces variables allant d'environ 0.12ha (*e.g.* surface ayant pour diamètre la distance maximale de 20m entre 2 pièges à interception pour les relevés d'insectes) à 3ha (rayon de 100m considéré pour les relevés d'oiseaux). Ces surfaces sont purement indicatives, car pour ces organismes mobiles, les valeurs de biodiversité observées reflètent un environnement plus large,

incluant notamment d'autres milieux favorables comme les milieux ouverts ou humides à proximité des zones échantillonnées qui pourraient avoir une influence non négligeable sur certains groupes (*e.g.* Bouvet et al., 2016; Miklín et al., 2018). Par exemple, Bouget et al. (2014), sur un échantillon recoupant partiellement celui utilisé dans Paillet et al. (in press) montrent, grâce à des relevés rapides d'habitat sur 1ha, que les densités d'arbres à cavités et porteurs de champignons influencent significativement la richesse et la composition en coléoptères saproxyliques. Nous n'avons pas obtenu de résultat comparable dans notre analyse, pour laquelle les microhabitats relevés sur 0.12ha expliquent assez peu la richesse et l'abondance des coléoptères, malgré un lien fonctionnel assez bien établi (Bouget et al., 2008; Larrieu et al., 2018). Pour des éléments rares comme les cavités ou les carpophores de champignons, on peut penser que des placettes de plus grande échelle permettent une meilleure évaluation de leur abondance, qui, en retour, retranscrit mieux la ressource disponible pour les coléoptères. Cependant, nous avons montré, pour les autres groupes étudiés, qu'il existait une relation à plus petite échelle entre structure forestière et biodiversité des oiseaux et chauves-souris, malgré les larges domaines vitaux de ces taxons (voir aussi Bouvet et al., 2016; Laiolo et al., 2004).

5.1.2.2 Quelles méthodes ?

Les méthodes utilisées pour quantifier les microhabitats comme la biodiversité restent imparfaites. Pour les microhabitats, les solutions permettant de réduire l'effet observateur et les biais de détection ont été abordées dans Paillet et al. (2015a) mais peu mises en œuvre pour les relevés constituant le cœur de mon travail de thèse. Pour les inventaires de microhabitats comparant forêt exploitées et non exploitées, nous avons limité le nombre d'observateurs (Paillet et al., 2017; Paillet et al., in press) mais ceux issus du réseau des réserves forestières Paillet et al. (preprint) ont été effectués dans des conditions peu contrôlées, par des observateurs aux sensibilités différentes (forestiers, gestionnaires d'espaces protégés, étudiants…). D'autre part, les indices de microhabitats utilisés sont également imparfaits, dans la mesure où c'est essentiellement la densité d'arbres porteurs qui est mesurée et non la densité réelle : les relevés par arbres sont en présence-absence de microhabitats et non en abondance (Paillet et al., 2017). Il faut donc considérer ces relevés comme assez bruités, au regard des méthodes standardisées qui ont été proposées par la suite (Larrieu et al., 2018). Cela semble se traduire par des taux d'accumulation de microhabitats en fonction du diamètre plus faibles que ceux observés ailleurs (Großmann et al., 2018; Regnery et al., 2013b; Vuidot et al., 2011).

Enfin, les méthodes d'inventaire de la biodiversité utilisées dans Paillet et al. (in press) sont plutôt destinées à évaluer l'activité des animaux, puisqu'elles reposent en partie sur leur mobilité (vol pour les coléoptères saproxyliques, écholocation pour les chauves-souris) ou leur activité au sens large (chant pour les oiseaux). De ce fait, ces méthodes sont biaisées vers les espèces les plus actives ou abondantes (*e.g.* la Pipistrelle commune, le Pinson des bois, ou les scolytes).

5.1.2.3 L'ambiguïté des standards

Dans l'idéal, l'ensemble des données utilisées dans ce travail de thèse aurait dû être basé sur la typologie présentée (Larrieu et al., 2018). Cette standardisation étant intervenue bien après qu'aient commencé les relevés de microhabitats (2008 sur le jeu de données comparant forêts exploitées et non exploitées, 2010 pour le test d'effet observateur et 2005 pour le jeu de données réserves), les typologies que nous avons utilisées sont moins précises (*cf.* Tableau 1). Par exemple, il y a trois types de cavités dans la typologie du jeu de données réserves, cinq dans Vuidot et al. (2011, typologie utilisée pour les comparaisons entre forêts exploitées et non exploitées) contre quinze dans Larrieu et al. (2018). Ce manque de précision a deux conséquences antagonistes : d'une part, il ne permet pas de relier précisément la biodiversité à des microhabitats spécifiques (*e.g.* lorsque les cavités de pics ne sont pas différenciées en fonction de leur taille), mais fournit d'autre part des nombres d'occurrences par type de microhabitat suffisants pour procéder à des analyses. Ce dernier point peut aussi être contourné en faisant des regroupements sur la base de typologies plus précises (voir par exemple

Larrieu et al., 2014b), mais l'analyse du lien entre types précis de microhabitats et biodiversité nécessite des jeux de données plus conséquents, qui ne peuvent s'obtenir que grâce à des suivis de grande ampleur (à l'image de celui coordonné par les Réserves Naturelles de France ou de l'Institut Forestier Européen, Kraus et al., 2017) ou qu'au travers d'approches collaboratives (Larrieu et al., 2014b). Ainsi, l'établissement de standards précis nécessite des échantillonnages plus intensifs et forcément plus coûteux pour répondre à des questions équivalentes, surtout lorsqu'on vise les grains les plus fins de ces standards. La nature hiérarchique de la typologie proposée ici (Larrieu et al., 2018) est censée pallier à ces difficultés, mais devra être suffisamment vulgarisée auprès des gestionnaires pour être adoptée et ne résoudra que partiellement la problématique de la granularité du relevé.

Au final, les incertitudes associées à la fois à la mesure des microhabitats (Paillet et al., 2015a), et à la mesure de la biodiversité (voir discussion dans Paillet et al., in press) font que cette relation statistique est fortement bruitée, mais semble malgré tout relativement solide. Ce bruit sera d'autant plus réduit que les méthodes de relevés des microhabitats seront standardisées (Larrieu et al., 2018; Paillet et al., 2015a), et les méthodes de suivi de la biodiversité le mieux adaptées aux espèces.

5.1.3 Les microhabitats, nouveaux indicateurs de biodiversité ?

Les microhabitats sont considérés comme des indicateurs structuraux indirects (proxies) d'une partie de la biodiversité forestière. A ce titre, ils présentent les mêmes écueils que d'autres indicateurs de ce type. Ainsi, si un lien, partiellement fonctionnel, avec certains *indicanda* a été mis en évidence (Paillet et al., in press), il n'en reste pas moins fondé sur une corrélation statistique non causale. Cependant, il me semble que cette approche par corrélation sera difficile à dépasser et qu'une validation expérimentale du lien causal entre une diversité de microhabitats et la biodiversité de groupes taxonomiques mobiles comme les oiseaux et les chauves-souris est assez illusoire, mais peut néanmoins s'envisager sur des microhabitats individuels (Cockle et al., 2010; Gossner et al., 2016; Lindenmayer et al., 2009). Condamnés à une approche corrélative, les indicateurs indirects de biodiversité ont cependant l'avantage d'être relativement faciles à mesurer ou à observer, avec des niveaux d'expertises moindres que la taxonomie et avec des coûts souvent limités par rapport à des relevés directs de biodiversité. Cependant, cette approche fondée sur la ressource disponible pour une espèce ou un groupe d'espèces néglige très largement les processus démographiques qui façonnent les communautés. En effet, ce n'est pas parce qu'un habitat est présent qu'il est occupé par les espèces, car elles n'ont pas encore colonisé ce milieu favorable, ou au contraire, la présence d'espèces en lien avec un habitat favorable peut n'être que temporaire car les populations sont en train de s'éteindre. Ces deux phénomènes sont connus respectivement sous les noms de crédit de colonisation et de dette d'extinction (Hanski & Ovaskainen, 2002). La connaissance de ces tendances de populations est insoluble par des indicateurs indirects et ne peut s'affranchir d'un suivi direct de la biodiversité (Gosselin et al., 2012; Paillet, 2017; Paillet et al., 2013). On atteint ainsi les limites des indicateurs indirects desquelles mon cas d'étude ne s'affranchit pas. Les microhabitats restent cependant un indicateur accessible aux gestionnaires, au contraire de groupes d'espèces qui nécessitent des compétences généralement pointues. Une fois ces limites identifiées, un certain nombre de points abordés dans ma thèse méritent d'être rappelés.

L'établissement d'une typologie de référence constitue un premier pas vers la validation des microhabitats en tant qu'indicateurs de biodiversité. Cette typologie se veut avant tout pratique et utilisable dans un panel de situations différentes. Bien que fondée sur la relation entre microhabitats et biodiversité de plusieurs groupes taxonomiques, le lien avec les théories écologiques reste peu établi. Les microhabitats sont considérés comme une partie de la niche écologique des espèces, mais leur contribution à la niche pour un groupe ou une espèce donné reste largement inconnue et probablement très variable : les dendrothelmes ou les cavités à terreau représentent sans doute une grande partie de la niche pour les espèces qui en dépendent (Gossner et al., 2016; Ranius et al., 2011), mais d'autres cavités représentent une partie plus modérée pour des espèces qui les utilisent

seulement pour gîter (*e.g.* certains mammifères, incluant les chauves-souris et oiseaux, Cockle et al., 2011; Tillon & Aulagnier, 2014). De fait, la théorie de la niche, qui traduit un ensemble de conditions favorables à des espèces données, retranscrit assez mal le lien entre microhabitats et biodiversité. Il serait sans doute plus pertinent d'évoquer la relation ressource-espèces (Bouget, 2013) ou l'hypothèse de quantité d'habitat qui traduit mieux le lien entre biodiversité et ressource (Seibold et al., 2016). Il semble d'ailleurs que la plupart des indicateurs de biodiversité forestière soient fondés – souvent implicitement – sur ces relations plus que sur la théorie de la niche.

D'autre part, la sensibilité des inventaires de microhabitats à l'effet observateur pourrait apparaitre rédhibitoire au regard du ratio signal / bruit lié à leur détermination par des publics différents. Bien que légitime, cette critique peut également s'appliquer à d'autres mesures utilisées en routine, pour lesquelles des niveaux comparables ont été démontrés (*e.g.* Larjavaara & Muller-Landau, 2013 dans le cas de la mesure de hauteur des arbres) ou n'ont jamais été quantifiés (*e.g.* mesure de quantités de bois mort). Il semble important de rappeler que ce travail partait du principe que ces relevés étaient réalisables par des observateurs non experts (Regnery et al., 2013b), ce qui, au final a concouru en grande partie à la diversité des résultats observés. Nous avons par ailleurs proposé des solutions pour faire en sorte que l'effet observateur soit minimisé dans les relevés futurs, ou a minima pris en compte dans les analyses statistiques. Si cet effet observateur mérite une vigilance particulière, il convient néanmoins de le mettre en perspective au regard de la typologie publiée en 2018 et de l'utilisation qui en sera faite à l'avenir (notamment des différents grains).

Les travaux sur l'influence de différents facteurs à l'échelle de l'arbre et de la parcelle forestière ont montré un lien fort entre les caractéristiques de l'arbre (diamètre, essence, vitalité) et les microhabitats, qui se retranscrivent au niveau de la parcelle forestière. Ainsi la présence de gros arbres et d'arbres morts en plus grande quantités dans les réserves intégrales (Paillet et al., 2015b) favorise de plus grandes densités de microhabitats. Ces résultats ont été confirmés par l'approche incluant la biodiversité (Paillet et al., in press), pour laquelle nous avons montré l'effet de médiation des microhabitats sur une partie de la biodiversité étudiée, ce qui constitue un prérequis indispensable à la validation « scientifique » d'un indicateur de biodiversité (Heink & Kowarik, 2010b). Cependant, la magnitude observée reste modeste au regard du gain en biodiversité et limitée à certains groupes.

De manière synthétique, on peut reporter les avancées de ce travail de thèse dans le tableau de Niemeijer and de Groot (2008) qui classifie les critères de validation des indicateurs environnementaux (Tableau 23). Au-delà des aspects purement « scientifiques » qui constituent le cœur de mon travail (notamment le lien indicateur-*indicandum*), les autres critères peuvent être complétés de manière plus qualitative. Cette grille d'analyse montre que l'indicateur microhabitat remplit assez bien un certain nombre de ces critères, bien que quelques-uns restent à consolider. Elle met aussi en évidence les lacunes de connaissance et un certain nombre de perspectives de recherches qui seront abordées ci-après.

Dimension	Critère	Description	Pour les microhabitats
Scientifique	Pertinence analytique	Solides bases scientifiques et conceptuelles	Bases théoriques assez faibles, mais de nombreuses références documentent le lien avec la biodiversité (Annexe 1)
	Crédibilité	Scientifiquement crédible	Existence d'un standard scientifiquement fondé (Larrieu et al., 2018)
	Caractère intégrateur	L'indicateur ou le système d'indicateurs doit couvrir des aspect / composants / gradients clés	Relativement universel, mais à adapter à d'autres biomes (Larrieu et al., 2018)
	Importance générale	Repose sur un processus fondamental ou un changement largement répandu	Pas étudié
Historique	Données historiques	Existence de données historiques comparables	Non
	Fiabilité	Antécédents éprouvés	Non
Systémique	Anticipatif	Annonce un changement imminent d'une caractéristique clé du système	Non
	Prévisible	Répond d'une manière prévisible à des changements et des contraintes	Oui à l'échelle de l'arbre (Paillet et al., preprint) à préciser à l'échelle de la parcelle (Paillet et al., 2017)
	Robuste	Relativement insensible à des sources d'interférences	Sensible à l'effet observateur (Paillet et al., 2015a) et variable en fonction de l'altitude (Paillet et al., 2017)
	Sensibilité à la contrainte	Sensible aux contraintes exercées sur le système	Sensible à l'exploitation forestière (Paillet et al., 2017)
	Spatialisation	Sensible aux changements spatiaux	Pas étudié
	Temporalité	Sensible aux changements temporels	Etudié de manière indirecte (Paillet et al., 2017)
	Niveau de connaissance	Un faible niveau de connaissance de l'indicateur veut dire qu'il y a beaucoup à gagner à l'étudier	Bonne connaissance *a priori*
Intrinsèque	Mesurabilité	Mesurable en termes quantitatifs ou qualitatifs	Oui
	Portabilité	Répétable et reproductibles dans différents contextes	Oui (mais voir Paillet et al., 2015a)
	Spécificité	Clairement et explicitement défini	Oui, depuis Larrieu et al. (2018)
	Propriétés statistiques	Les propriétés statistiques permettent une interprétation sans ambigüité	Oui, mais dépend de l'indice (microhabitat, biodiversité) utilisé. Magnitude faible de la relation biodiversité / microhabitat)
	Universalité	Applicable dans de nombreuses contextes : régions, situations, et échelles	Oui, mais nécessite des adaptations typologiques
Pratique et financière	Coûts, bénéfices et rapport coût-bénéfice	Les bénéfices de l'information fournie par l'indicateur surpassent son coût d'usage	Non étudié
	Besoin et disponibilités des données	Recueil de données facile à gérer ou données déjà existantes et disponibles	Non, mais voir (Kraus et al., 2017)
	Compétences nécessaires	Ne nécessite pas des compétences excessives pour l'acquisition de données	A tester sur la nouvelle typologie (Paillet et al., 2015a)
	Opérationnalité et simplicité	Simple à mesurer, à gérer et à analyser	Oui
	Ressource nécessaire	Réalisable dans la mesure des ressources disponibles	Oui, mais à évaluer précisément et dépendant du contexte local
	Temps nécessaire	Réalisable dans la mesure du temps disponible	Oui, mais à évaluer précisément en fonction du grain et du contexte local
Politique et gestion	Compréhensible	Simple et facilement compréhensible par l'audience cible	Oui, mais à évaluer précisément
	Compatible à l'international	Compatibilité avec les indicateurs développés et utilisés dans d'autres régions	Oui, si adaptation typologique (*cf.* Kraus et al., 2016)
	Lien avec la société	Connectable aux développements socio-économiques et aux indicateurs sociétaux	Pas étudié (sciences participatives ?)
	Lien avec la gestion	Liens bien établis avec des pratiques de gestion ou interventions spécifiques	Oui dans le cas de la mise en réserve. A voir pour d'autres modes de gestion
	Progrès vers une cible	Liens qualitatif ou quantitatif avec des objectifs fixés par les documents politiques	Pas actuellement
	Quantification	L'information doit être quantifiée d'une façon à ce que sa significativité soit apparente	*A priori* oui
	Pertinence	Pertinence pour la problématique et l'audience concernée	Oui, à évaluer précisément
	Applicabilité spatiale et temporelle	Fournit de l'information aux bonnes échelles spatiales et temporelles	Informatif à l'échelle d'une réserve. L'influence de l'échelle de relevé reste à tester
	Seuils	Existence de seuils pouvant être utilisés pour déterminer quand agir	Partiellement, voir *e.g.* Larrieu et al. (2012)
	Conçu par les utilisateurs	Conçu ou émane des utilisateurs pour être pertinent pour l'audience cible	Non, mais adopté assez largement (Kraus et al., 2016)

Tableau 23 : Critères de sélection et d'utilisation des indicateurs environnementaux appliqué au cas des microhabitats (d'après Niemeijer et de Groot, 2008).

On peut donc considérer, au regard de ce travail et des publications récentes sur le sujet, que les microhabitats peuvent constituer un (nouvel) indicateur de biodiversité forestière. Ce ne sont cependant pas un indicateur universel et ils semblent jouer un rôle complémentaire – ou intermédiaire – à d'autres indicateurs utilisés classiquement pour évaluer la biodiversité (bois mort, gros arbres). Ils présentent des qualités intéressantes, et notamment un lien fonctionnel avec des pans de biodiversité peu évalués par d'autres indicateurs (animaux cavicoles, insectes des dendrothelmes), mais aussi une applicabilité directe à la gestion forestière. Ces travaux confirment par ailleurs que l'indicateur universel n'existe de toutes façons pas (Heink & Kowarik, 2010b) et que des évaluations environnementales gagnent à être fondées sur des systèmes multi-indicateurs explicitement mis en relation avec des objectifs clairs dans un cadre d'analyse donné (*cf.* 5.2.2.4). Ces aspects mettent en évidence la nécessité de poursuivre des travaux de recherche, à la fois sur les microhabitats, mais aussi sur les indicateurs de biodiversité et environnementaux.

5.2. Perspectives de recherche

5.2.1 Sur les microhabitats

5.2.1.1 Mieux comprendre leur distribution et leur dynamique

La première perspective de recherche est liée à l'établissement de la liste de référence présentée ici : il s'agit de continuer à réduire les incertitudes liées aux inventaires de microhabitats. Les effets observateurs mesurés sur les listes précédentes sont forts, et il peut également y avoir une variabilité des relevés en fonction des conditions locales (météo, relief, végétation…). Il semble intéressant de quantifier ces biais potentiels sur cette nouvelle typologie, avec des publics différents, soit professionnels (forestiers, responsables d'inventaires forestiers), soit généralistes (gestionnaires d'espaces naturels, étudiants) de manière à mieux évaluer la faisabilité de ces inventaires et le bruit associé à ces mesures. La nature hiérarchique de la typologie de Larrieu et al. (2018) permettrait également de quantifier le biais d'observation lié aux différents grains, de manière à analyser leur pertinence au regard des usages qui en ont été proposés (*e.g.* martelages, inventaires de gestion ou scientifiques).

Sur les bases communes de cette typologie, il semble désormais possible de compiler des bases de données recouvrant de larges gradients écologiques (sur le modèle de Kraus et al., 2017). L'analyse de telles bases permettrait de généraliser les résultats obtenus à l'échelle de l'arbre à d'autres contextes. En premier lieu, il serait intéressant de mieux comprendre les effets des variables environnementales (en particulier climatiques et topographiques) sur la présence et la dynamique des microhabitats. Ce travail est possible sur des espèces d'arbres à large spectre écologique (*e.g.* hêtres, pins) pour éviter la confusion entre conditions environnementales et espèce d'arbre. Des espèces (et des genres) d'arbres étant présentes hors de l'Europe et jusqu'en Asie ou outre-Atlantique (chênes, hêtres, par exemple), ces travaux pourraient être étendus et généralisés à d'autres biomes, dans des conditions variées de manière à voir si les relations observées en Europe sont liées aux conditions environnementales ou à l'espèce (au genre), ou encore à une combinaison de ces deux facteurs. La large diffusion de la typologie initiale par l'Institut Forestier Européen (Kraus et al., 2016) et son accessibilité aux gestionnaires semblent prometteuse à cet égard et devrait permettre une meilleure prise en compte des microhabitats dans la gestion forestière en Europe et au-delà (la typologie a récemment été traduite en farsi). D'autre part, il semble désormais acquis que le diamètre a une influence positive forte sur la plupart des microhabitats. Cet effet est indirectement attribué à l'âge des arbres qui, s'ils sont plus gros, ont aussi des chances d'être plus vieux et d'avoir subi plus de dommages générateurs de microhabitats (Bobiec et al., 2005; Vuidot et al., 2011). Cependant, les effets respectifs de l'âge et du diamètre n'ont pour le moment pas été démêlés et restent un champ de recherche largement ouvert. Enfin, une meilleure compréhension des corrélations entre types de microhabitats (Regnery et al., 2013b) devrait permettre d'identifier, sur la base de co-occurrences, des

types de microhabitats « clés de voûte » dont la présence conditionne celle d'autres types. Cette approche corrélative pourrait également permettre de simplifier la typologie sur une base analytique.

A l'échelle de la parcelle, les premières références établies dans Paillet et al. (2017) viennent compléter le travail déjà accompli au cours de la dernière décennie (Larrieu et al., 2014b ; Winter & Möller, 2008). Cependant, le gradient d'abandon d'exploitation considéré dans ce travail reste relativement limité (au maximum 150 ans d'arrêt exploitation) et ne permet pas de comprendre la dynamique des microhabitats sur le long terme, à l'échelle du cycle silvigénétique. Un travail similaire sur les rares forêts considérées comme primaires en Europe (Commarmot et al., 2013; Sabatini et al., 2018) viendrait compléter cette approche et fournir des données de référence pour la recherche (voir Kozák et al., 2018 en Annexe E), voire à établir des objectifs de gestion forestière dans une approche normative (Heink & Kowarik, 2010b). De la même manière, sur un gradient d'exploitation, il serait intéressant d'affiner le lien entre traitements sylvicoles (ou modalités de gestion) et distribution et dynamique des microhabitats (Courbaud et al., 2017; Larrieu et al., 2014b). Même si elle n'est pas aisée *a priori*, la comparaison de la distribution des microhabitats dans des futaies régulières et irrégulières dans des conditions similaires (*e.g.* à l'image des travaux de Schall et al., 2018) permettrait d'éclairer les choix de gestion intégrant les microhabitats comme outil de préservation de la biodiversité. Ce type d'analyse pose inévitablement la question de la dynamique spatiale et temporelle des microhabitats, dans la mesure où les sylvicultures évoquées ne maintiennent pas le couvert forestier de la même manière (intermittent à l'échelle d'une révolution en futaie régulière, continu en futaie irrégulière).

Enfin, bien qu'abordée de manière synchronique dans ce travail de thèse (Paillet et al., 2017), la compréhension de la dynamique temporelle et la construction de modèles d'évolution (Courbaud et al., 2017) ne pourra s'affranchir d'un suivi temporel des microhabitats à l'image de celui réalisé par le réseau des réserves naturelles (*cf.* Paillet et al., preprint).

5.2.1.2 Consolider le lien avec la biodiversité

Les travaux qui ont tenté de faire le lien entre listes de microhabitats et biodiversité restent pour le moment rares et limitées à certains groupes taxonomiques, dont ceux traités ici (Paillet et al., in press). Si d'autres groupes ont été traités dans d'autres régions du monde, notamment les oiseaux cavicoles (Cockle et al., 2011; Martin et al., 2004) ou certains marsupiaux par exemple (Lindenmayer et al., 2017), le lien pratique avec la gestion forestière est plus ténu dans le cas de ces travaux. Au regard de la variété des organismes dépendants des microhabitats (Larrieu et al., 2018; Siitonen, 2012), il semble intéressant de poursuivre les recherches sur d'autres groupes taxonomiques, afin de compléter les connaissances sur les microhabitats. Ce type d'échantillonnage pourrait utiliser des méthodes classiques (points d'écoutes, capture des insectes mobiles, pièges photographiques), ou des méthodes ciblées sur certains microhabitats, *e.g.* piégeages sur carpophores (Gouix & Brustel, 2012), occupation de cavités (Martin et al., 2004; Martin & Eadie, 1999; Robles & Martin, 2014; Wesołowski et al., 2010), ou des combinaisons de ces méthodes afin d'obtenir une meilleure représentation de la diversité associée. Dans cette optique, le développement de méthodes basées sur l'ADN environnemental (metabarcoding) semble prometteur. Il est également possible de promouvoir une approche expérimentale manipulant, à l'échelle de la parcelle forestière des quantités et des qualités de certains microhabitats relativement faciles à reproduire : *e.g.* dendrothelmes (Gossner et al., 2016) ou cavités (Lindenmayer et al., 2009). L'ensemble de ces recherches permettrait une vision plus exhaustive de la biodiversité associée à certains types de microhabitats, notamment celle qui n'est pas captée par des échantillonnages classiques (*e.g.* espèces fongicoles par exemple), mais également d'approcher les mécanismes d'utilisation des microhabitats par la biodiversité associée (*e.g.* Cockle et al., 2011).

Au regard des relations différentes entre biodiversité et microhabitats obtenues avec des placettes de tailles variables (*cf.* Bouget et al., 2014; en comparaison avec Paillet et al., in press par exemple), il semble intéressant d'avoir des approches avec des surfaces d'échantillonnage variables pour identifier

le meilleurs compromis d'échelle en termes de ratio signal/bruit (à l'image de Lombardi et al., 2015). De telles approches, en lien avec des relevés de biodiversité pourraient également permettre de déterminer la taille d'habitat optimale pour une espèce ou une guilde donnée (sensu Fahrig, 2013). Ces perspectives d'échelle ouvrent sur une autre lacune, mise en évidence dans le Tableau 23, et qui concerne les patrons spatiaux auxquels répondent les microhabitats, notamment en l'absence d'exploitation forestière. L'étude de la répartition des microhabitats et des facteurs qui l'influencent permettrait d'informer la mise en œuvre d'une gestion conservatoire. De telles recherches abonderaient au débat dit SLOSS (Single Large vs Several Small, Fahrig, 2013; Ovaskainen, 2002) dans le cas des microhabitats, au regard d'une biodiversité cible : en effet, à l'heure actuelle, il est difficile de dire si les effets de la conservation d'une grande diversité de microhabitats portée par un seul arbre est équivalente à une diversité identique mais portée par des arbres différents (*cf.* Le Roux et al., 2015). En ce sens, le test d'hypothèses de quantité d'habitat (Fahrig, 2013) à l'échelle d'une trame de vieux bois intra-forestière apparaît comme un front de recherche à la fois stimulant mais difficile à traiter.

Cet ensemble de perspectives, illustrées ici sur le cas des microhabitats, peuvent s'appliquer sur un large panel d'indicateurs de biodiversité (forestière), notamment ceux de Forest Europe, pour la plupart desquels le lien avec la biodiversité reste assez peu documenté (Gao et al., 2015). Mais au-delà d'une diversification des indicateurs et des *indicanda*, il semble intéressant de questionner les perspectives de recherche sur l'objet indicateur, avec un focus spécifique sur les indicateurs environnementaux ou de biodiversité.

Principales perspectives de recherche sur les microhabitats

<u>Méthodologiques</u>

Quantifier l'effet observateur à différents grains de la nouvelle typologie et pour différents usages (martelage, inventaires de routine…)

Tester l'effet de l'échelle de relevé sur la précision des inventaires

<u>A l'échelle de l'arbre</u>

Diversifier les contextes dans lesquels sont testés les relations entre microhabitats et caractéristiques des arbres

Comprendre l'effet des variables environnementales sur les essences largement répandues

Démêler l'effet âge de l'arbre de l'effet diamètre

<u>A l'échelle de la parcelle forestière et de la forêt</u>

Etablir des références en forêts primaires ou non exploitées depuis plusieurs décennies

Tester l'effet de différentes modalités de gestion et de traitements sylvicoles

Comprendre la dynamique spatiale et temporelle, dans un contexte de gestion et d'abandon de gestion

<u>Lien avec la biodiversité</u>

Elargir le champ taxonomique

Tester la robustesse

Expérimenter sur des microhabitats « manipulables »

Tester l'influence de l'échelle

5.2.2 Sur les indicateurs

5.2.2.1 Importance de l'indice dans le couple indicateur / indicandum

Le processus de validation d'un indicateur est inhérent au couple indicateur / *indicandum* qui est évalué. Dans ce couple, les indices utilisés pour caractériser l'indicateur et l'*indicandum* revêtent une place primordiale (*e.g.* Lamb et al., 2009; Noss, 1990). La plupart des indicateurs indirects de biodiversité (forestière) sont des indices d'abondance (*e.g.* volume de bois mort, quantité d'habitat favorable…). Ils reposent sans doute en grande partie sur l'hypothèse énergie-espèce qui prédit qu'une augmentation de la quantité d'habitat ou de ressource disponible engendre une augmentation de la richesse locale (*e.g.* Fahrig, 2013). Cependant, les préconisations de gestion, comme l'hypothèse d'hétérogénéité (Seibold et al., 2016; Tews et al., 2004), insistent avant tout sur la diversité d'habitats comme moteur de la diversité d'espèces. Ainsi, les indicateurs reposant sur des indices de diversité (*e.g.* indice de Shannon des types de bois mort) sont plus rares bien qu'apparemment plus fondés sur des pratiques de gestion ou sur des bases théoriques : des études comparant leur performance à des indicateurs basés sur des indices d'abondance pourraient être entreprises.

D'autre part, il est sans doute illusoire de rechercher un indicateur universel qui permettrait de décrire les variations précisément et sans équivoque un large panel de taxons ou de conditions environnementales (Heink & Kowarik, 2010a; Heink & Kowarik, 2010b). Une des solutions consiste à définir des indicateurs composites qui agrègent deux variables ou plus (*cf.* Moriarty et al., 2018 pour des exemples en écologie marine). De tels indices ont l'avantage de résumer des processus complexes en une valeur unique, et constituent un bon outil de gestion et de communication en raison de leur simplicité apparente (Becker et al., 2017; Moriarty et al., 2018). Par exemple, l'Indice Biotique Global Normalisé agrège la présence de certaines espèces de macroinvertébrés aquatiques sensibles à des pollutions et la richesse faunistique d'un site. Il est utilisé pour déterminer la qualité biologique d'un cours d'eau et permet de calculer une note de qualité de l'écosystème (Bouleau, 2016). Cet indice est normalisé et fait foi dans la directive cadre sur l'eau. En forêt, une des rares initiatives équivalentes de bioindication implique les Syrphes (base de données Syrph-The-Net, Speight et al., 2013) et des travaux équivalents sont en cours pour les coléoptères saproxyliques (T. Noblecourt, Comm. Pers.), sans pour autant avoir atteint la norme imposée par l'indice biotique. Plus généralement, les indices composites, notamment ceux mobilisant des données de structure forestière – potentiellement plus complexes que l'exemple fourni ci-dessus car utilisant des unités différentes – sont à ce jour absents de processus de rapportage internationaux au bénéfice d'indicateurs basés sur un indice unique et de faisceaux d'indicateurs censés décrire des pans différents de biodiversité (*cf.* sections 1.3.1 et 5.2.2.4).

De tels indicateurs composites, comme ceux basés sur des indices de diversité, sont sans doute plus difficiles à interpréter que ceux basés, par exemple, sur des indices simples d'abondance. Les indicateurs composites posent également la question de la pondération éventuelle accordée aux différentes composantes (*cf.* Becker et al., 2017). C'est sans doute pour ces raisons qu'ils ne sont pas plus répandus, mais une réflexion plus systématique sur leur développement serait intéressante.

5.2.2.1 Robustesse ou contextualisation ?

La capacité de l'indicateur à garder un lien avec l'*indicandum* malgré les interférences est souvent cité comme un critère de validation important (Moriarty et al., 2018; Niemeijer & de Groot, 2008). Cette notion de robustesse implique, implicitement, qu'il n'y a pas de variation de la relation, que ce soit de direction, de magnitude ou de significativité, avec le contexte et que l'indicateur serait valable, partout, de la même façon. Il semble néanmoins assez irréaliste de considérer une relation – biologique – comme immuable dans le temps et dans l'espace (Heink & Kowarik, 2010b). Concrètement, les bases empiriques qui ont poussé à choisir le bois mort comme indicateur de biodiversité forestière au niveau européen étaient à l'origine issues d'études réalisées en Scandinavie (Bouget, 2013; Lassauce et al., 2011). Les progrès récents de connaissance dans les forêts tempérées montrent que cette relation n'est pas forcément partout aussi solide – ni forte – que ce qui était pressenti par les études dans les

milieux boréaux (voir la discussion dans Lassauce et al., 2011). Ainsi, la notion de robustesse d'un indicateur, de même que sa fiabilité et sa représentativité, semblent pouvoir être remises en cause au profit d'une contextualisation (Zilliox & Gosselin, 2014), plutôt que de l'invalidation d'un indicateur qui ne serait plus valable dans certaines situations. Il me semble en effet plus intéressant de rechercher comment les liens entre indicateurs et *indicanda* varient en fonction de différents facteurs, à commencer par des facteurs biogéographiques, de manière à informer plus précisément les politiques de conservation et les actions de gestion.

5.2.2.2 Forme de la relation entre indicateur et indicandum

La forme de la relation entre indicateur et *indicandum* semble assez peu abordée dans la littérature scientifique, voire totalement absente des processus de rapportage internationaux. Il est généralement supposé qu'un accroissement de la quantité de l'indicateur entraine une augmentation de l'*indicandum* (ou inversement, suivant la nature de l'indicateur). Or, la plupart des modèles statistiques utilisés pour étudier ce lien assument une réponse non saturante (sans asymptote). C'est particulièrement vrai pour les indicateurs de biodiversité pour lesquels l'analyse de variables de comptage (comme la richesse spécifique ou l'abondance) impliquent par défaut, dans un contexte fréquentiste, une fonction de lien exponentielle liée à une distribution d'erreur Poissonnienne. Cette approche apparait contestable pour au moins deux raisons :

- D'une part, à surface constante, il semble irréaliste de supposer qu'une augmentation de la quantité de ressource entraine une augmentation infinie de biodiversité (qu'elle soit linéaire ou exponentielle), qui par définition est une dimension finie. Cette critique se rapproche d'ailleurs de celles formulées par les économistes hétérodoxes à l'égard de certains indicateurs (comme le « produit intérieur brut ») sur lesquels se fondent le principe néoclassique de croissance économique continue et sans limites. En effet, ce principe, construit par analogie mathématique aux modèles physiques d'entropie, semble assez peu applicable à un monde réel où les ressources sont finies (Maris, 2003). Il semble donc délicat d'appliquer un raccourci similaire aux indicateurs environnementaux ;
- D'autre part, la relation aire-espèces et ses différentes extensions (notamment l'hypothèse de quantité d'habitat, Fahrig, 2013) est basée sur une relation puissance (saturante), qui, même si elle est relativement bien admise, est rarement utilisée pour analyser les données de biodiversité à l'échelle de la communauté, et plus généralement les relations entre espèces et ressources.

Même si elle peut entrainer des interprétations erronées (absence de saturation de l'*indicandum*), cette approche n'est cependant pas forcément rédhibitoire, et le raccourci a même peut-être été renforcé par des travaux sur des gradients tronqués de quantité d'habitat (Figure 13) : les relations observées ont pu paraitre linéaires ou partiellement exponentielles parce que les gradients étudiés n'étaient pas complets. Par exemple, si l'on étudie la relation entre volume de bois mort et espèces saproxyliques uniquement en forêt exploitée (donc sur un gradient tronqué de ressource), il est possible que l'effet de saturation ne puisse être détécté et que la relation paraisse linéaire. Il semble malgré tout intéressant de renforcer les approches basées sur d'autres formes de relation entre indicateur et *indicandum* (*cf.* Bouget, 2013), afin de retranscrire des relations plus réalistes et avec des bases théoriques solides. Ainsi, des formes puissance pourraient être testées, de même que des formes sigmoïdes qui supposent un point d'inflexion dans la relation (Gosselin, 2011). Ces approches mobilisent des méthodes statistiques bayésiennes (Clark, 2005) qui nécessitent, pour le moment, de fortes compétences analytiques et impliquent des jeux de données conséquents pour être performantes.

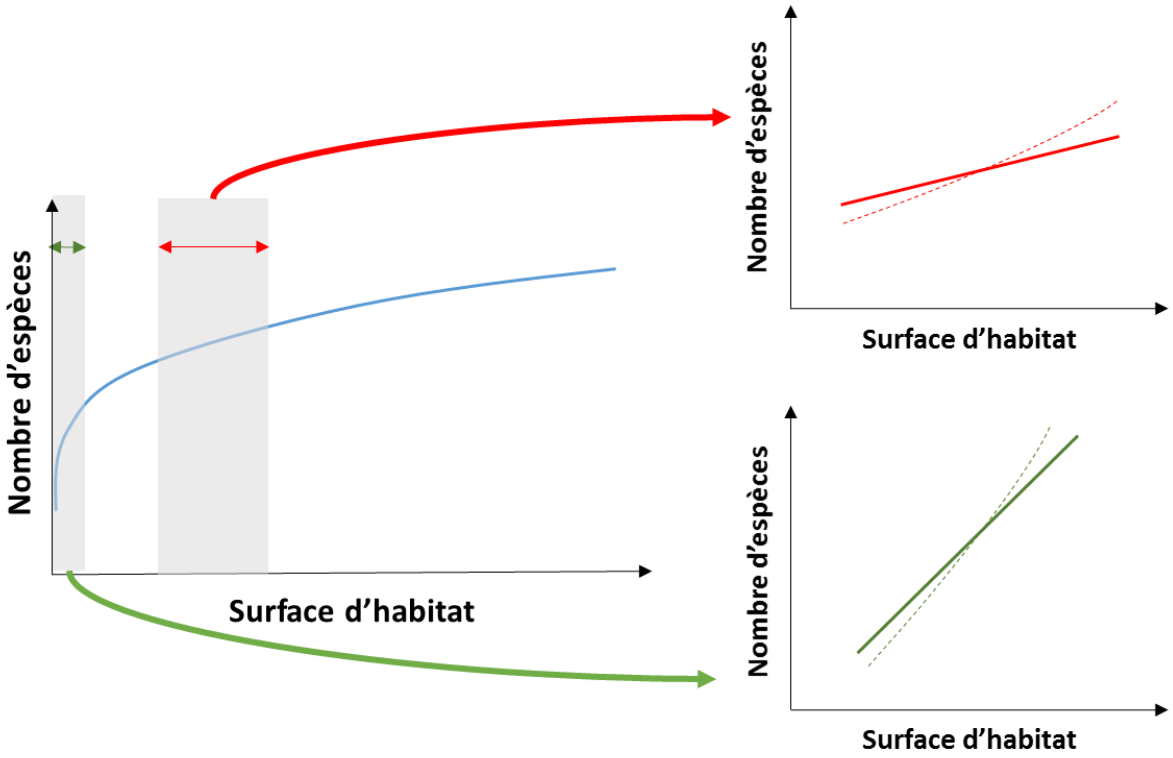


Figure 13 : Illustration du travail sur un gradient tronqué d'habitat : les relations entre nombre d'espèces et quantité d'habitat peuvent apparaitre linéaires alors que sur un gradient étendu, elles ne le sont plus.

Enfin, un cas particulier de forme de relation est la relation seuil (Herrmann et al., 2003; Samhouri et al., 2010). Ce type de relation, non continue, suppose l'existence d'un niveau d'indicateur à partir duquel on observe une variation significative de l'indicandum. De la même manière que les relations linéaires ou exponentielles, ce type de lien a peu de justifications théoriques (notamment la discontinuité de la relation par rapport aux gradients biologiques étudiés), mais des applications en matière de gestion et de politiques publiques évidentes, du fait de la clarté de la réponse apportée (*cf.* (*cf.* Larrieu et al., 2012 par exemple). Au regard de la portée normative de telles approches (Heink & Kowarik, 2010a), la mise en œuvre de ce type de modèles et la diffusion de tels résultats doivent malgré tout être accompagnés de précautions afin qu'ils ne soient pas retranscrits directement dans la gestion ou les politiques environnementales, sans lien avec le contexte dans lequel ils ont été produits. De ce fait, un travail conjoint impliquant des écologues, des gestionnaires et des politiques parait nécessaire (Heink & Kowarik, 2010b).

5.2.2.3 Lien avec l'indicandum : magnitude plutôt que corrélation ?

Dans leur synthèse, Heink and Kowarik (2010b) montrent l'importance qui est accordée à la corrélation entre indicateur et *indicandum* dans les travaux traitant d'une description scientifique de la biodiversité – à l'instar de mon travail de thèse. Ces auteurs montrent également que, dans les travaux traitant de validation politique d'indicateurs, ce n'est qu'un critère parmi d'autres (Tableau 23). De fait, des auteurs comme Niemela (2000) avancent que, pour qu'un indicateur soit validé, la corrélation entre indicateur et *indicandum* doit être significative et forte, sans pour autant préciser de seuil à partir duquel une corrélation est considérée comme telle. Si l'importance accordée à la significativité des résultats est largement remise en cause (*e.g.* Halsey et al., 2015), il n'en va pas de même pour la corrélation – au sens du pourcentage de variance expliquée – qui garde, aux yeux de nombreux écologues, une forte valeur validante d'un résultat statistique (Gosselin, 2011). Ainsi, des méthodes ont été proposées pour calculer des coefficients de corrélation pour des modèles mixtes généralisés

(pseudos-R^2) devenus populaires pour l'analyse de données en écologie (Bolker et al., 2009; Nakagawa & Schielzeth, 2013). Ces pseudos-R^2 prennent en compte les parts respectives de variances expliquées par la partie fixe (R^2 marginal) et aléatoire (R^2 conditionnel) d'un modèle (Nakagawa & Schielzeth, 2013). Cependant, pour des plans d'échantillonnages multi-sites, comme ceux analysés dans ce travail et qui nécessitent la prise en compte de facteurs non contrôlés par des effets aléatoires, ces approches fournissent en général des corrélations marginales faibles, car la majorité de la variation est expliquée par les différences entre sites. Il apparait donc difficile d'utiliser ce type de critère pour valider un indicateur, malgré la portée potentiellement plus générale d'une approche multi-site. De plus, il serait sans doute compliqué de promouvoir, auprès de gestionnaires ou de politiques, un indicateur présentant un très faible « lien » avec son *indicandum*.

Ainsi, l'approche mise en avant ici a plutôt insisté sur le sens et la magnitude (la force) des effets de l'indicateur sur l'*indicandum*, voir par exemple Barbier et al. (2009) et Zilliox and Gosselin (2014), mais sans pour autant adopter une approche par « négligeabilité » (Gosselin, 2011). L'avantage de l'approche par magnitude est qu'elle permet de quantifier l'effet d'une variation d'une variable explicative (de gestion, dans notre cas) sur une cible donnée, ce que ne permet pas un coefficient de corrélation. Cependant, les magnitudes assez faibles observées ici présentent la même difficulté que celle mentionnée sur le coefficient de corrélation, et pourraient freiner les gestionnaires à mettre en œuvre des pratiques ayant un effet potentiellement « négligeable » au sens de Gosselin (2011). L'approche par négligeabilité ne me parait ainsi pas un critère indispensable à la validation d'un indicateur mais plutôt à une priorisation du choix des indicateurs en fonction des objectifs visés. Par exemple, ce type d'analyse de magnitude pourrait conduire à préférer des indicateurs de biodiversité présentant des niveaux forts de leur lien avec l'*indicandum*, en fonction, par exemple, du taxon. Quoi qu'il en soit, les seuils différenciant une relation faible d'une relation forte devront être choisis sur des bases analytiques ou de gestion réalistes, clairement définies, voire négociées avec les utilisateurs dans un objectif d'application.

5.2.2.4 Rationaliser les processus de rapportages basés sur des systèmes d'indicateurs : cas des indicateurs de gestion forestière durable

Les systèmes d'indicateurs sont tout d'abord critiqués du fait du manque de définitions des enjeux qu'ils sont censés informer ou l'absence de précision sur les aspects qu'ils sont censés indiquer (Heink & Kowarik, 2010b; Niemeijer & de Groot, 2008). Par exemple, le terme de biodiversité est souvent cité comme cible d'indicateurs ou de systèmes d'indicateurs sans que la part de biodiversité qui est effectivement évaluée soit définie précisément (Feest, 2013; Heink & Kowarik, 2010b). Ensuite, les systèmes d'indicateurs, basés ou non sur une approche hiérarchique critères / indicateurs comme le sont les indicateurs de gestion forestière durable (Forest Europe, 2015a), sont évalués par leur capacité à répondre à des enjeux globaux mais sont rarement inscrits dans un cadre d'analyse *a priori* qui permettrait d'identifier des lacunes d'évaluation (comme le cadre Pression-Etat-Réponse par exemple, Niemeijer & de Groot, 2008). Lorsqu'ils sont construits sur la base d'un tel cadre d'analyse, comme le sont les indicateurs de l'Agence Européenne de l'Environnement, les relations causales potentielles qui lient ces indicateurs sont rarement explicitées (*cf.* Feest, 2013 pour les indicateurs de l'Agence Européenne de l'Environnement; et les travaux de Wolfslehner, 2007 sur les indicateurs de gestion forestière durable).

Pourtant, une telle classification n'est pas forcément complexe à mettre en œuvre sur une base experte : le Tableau 24 propose une classification des indicateurs de gestion forestière durable dans le système pression-état-réponse au regard de la biodiversité (forestière). Dans ce tableau, il est possible de préciser, pour les indicateurs de pression, la partie de biodiversité concernée (l'*indicandum*), le sens dans lequel l'indicateur influence l'*indicandum* et une qualification de la magnitude probable de la relation. L'analyse de ce tableau fournit ainsi un constat relativement clair :

- Tous les indicateurs ayant un lien potentiel avec la biodiversité ne se situent pas dans le critère 4 qui lui est dédié ;
- La plupart des indicateurs de gestion durable ayant un lien avec la biodiversité sont des indicateurs de pression (12/35), alors que seulement deux sont considérés comme des indicateurs directs d'état (taxonomiques) et six de réponse politique à une problématique de biodiversité ;
- Pour les indicateurs de pression, le lien avec la biodiversité (forestière) est variable d'un indicateur à l'autre et parfois au sein même d'un même indicateur suivant la partie considérée ou la part de biodiversité évaluée. Il existe plusieurs cas où des liens équivoques sont difficiles à mettre en évidence, quelle que soit la part de biodiversité considérée.

Indicateurs	Pression	Etat	Réponse
1.1. Surface forestière	Biodiversité (forestière) ++		
1.2. Stock sur pied	Biodiversité forestière +		
1.3. Structure d'âge et/ou distribution des diamètres	Biodiversité forestière +		
1.4. Stock de carbone			
2.1. Dépôt de polluants atmosphériques	Biodiversité (forestière) --		
2.2. Etat des sols	+/-		
2.3. Défoliation	+/-		
2.4. Dégâts forestiers	+/-		
3.1. Accroissement et exploitation	+/-		
3.2. Bois ronds			
3.3. Produits non ligneux			
3.4. Services (valeur)			
3.5. Forêts disposant d'un plan de gestion			X
4.1. Composition en espèces d'arbre		X	
4.2. Régénération	Biodiversité forestière --		
4.3. Naturalité	Biodiversité forestière : ++ (Forêts naturelles) -- (plantations d'espèces exotiques)		
4.4. Espèces d'arbre introduites	Biodiversité (Forestière) --		
4.5. Bois mort	Biodiversité forestière ++ (saproxyliques)		
4.6. Ressources génétiques			X
4.7. Paysage	Biodiversité forestière : -- (Espèces de cœur de massif ou à capacités de dispersion limitées)		
4.8. Espèces forestières menacées		X	
4.9. Forêts protégées			X
5.1. Forêts à fonction de protection – sol, eau et autres fonctions			
5.2. Forêts à fonction de protection – infrastructures et ressources naturelles exploitées			X
6.1. Propriété forestière			
6.2. Contribution du secteur forestier au produit intérieur brut			
6.3. Revenu net			
6.4. Dépenses de l'état en faveur des forêts			X
6.5. Emploi dans le secteur forestier			
6.6. Santé et sécurité dans le secteur des travaux forestiers			
6.7. Consommation de bois			
6.8. Commerce du bois			
6.9. Energie bois			
6.10. Accès au public			
6.11. Valeurs culturelles et spirituelles			X
Totaux	**12**	**2**	**6**

Tableau 24 : Classification des indicateurs de gestion durable forestière dans le cadre analytique Pression – Etat – Réponse au regard de la biodiversité. Sur fond gris, le critère 4 dédié à la biodiversité. Chaque indicateur a volontairement été classé dans une seule catégorie. Les parenthèses indiquent que la pression concerne à la fois les espèces généralistes et les spécialistes forestières. Les signes + et – renseignent sur la magnitude de la réponse potentielle de la biodiversité à une augmentation de la valeur de l'indicateur : -- négatif fort ; - négatif ; +/- non équivoque ; + positif ; ++ positif fort.

Cependant, ce type de classification peut également ouvrir des pistes de réflexions intéressantes, car une fois réalisée, il est tentant de rechercher, par des méthodes analytiques utilisant les modèles à équations structurelles (*i.e.* Paillet et al., in press), une confirmation des liens (causaux) associant les différentes catégories d'indicateurs dans le système pression-état-réponse. Même si cette approche s'avère probablement limitée par le manque d'indicateurs directs de biodiversité et par le caractère circulaire du système pression-état-réponse non pris en compte dans les modèles, il serait intéressant de vérifier si les liens (causaux) présumés sont confirmés par l'analyse des données européennes que rapporte Forest Europe tous les cinq ans (Forest Europe, 2015a). On peut noter également que ce processus se dotera en 2020 d'un dixième indicateur de biodiversité concernant les populations d'oiseaux forestiers (Forest Europe, 2015b), ce qui contribuera à enrichir l'approche et le rapportage. Enfin, la méthode mise en œuvre dans l'article de Paillet et al. (in press) pour les microhabitats pourrait s'appliquer à d'autres indicateurs issus de Forest Europe ou d'autres processus de rapportage.

Même si ces considérations dépassent assez largement le cadre de cette thèse, elles montrent qu'en forêt comme dans les autres secteurs, le cadre d'analyse et de validation des indicateurs de biodiversité est encore très partiel. Il est notamment facile de constater le manque d'indicateurs taxonomiques permettant de renseigner de l'état et de l'évolution de pans de biodiversité typiquement forestière (*e.g.* champignons, lichens, coléoptères saproxyliques) sur lesquels reposent les enjeux de gestion en faveur de la biodiversité (Gosselin et al., 2012; Paillet, 2017; Paillet et al., 2013). Par ailleurs, peu d'indicateurs ont bénéficié d'une analyse quantitative permettant d'établir le lien avec leur *indicandum* (voir Lassauce et al. (2011) dans le cas du bois mort, ou Gao et al. (2015) pour une perspective plus large) et une contextualisation de ce lien.

Principales perspectives de recherche sur les indicateurs

Comparer la performance d'indices de diversité avec des indices d'abondances

Construire des indices composites pour la forêt

Contextualiser plus systématiquement les indicateurs dans leur domaine d'application

Tester différentes formes de relation entre indicateur et indicandum (puissance, sigmoïde, seuil)

Définir, avec les utilisateurs, des niveaux de magnitude qui valideraient des indicateurs

Inscrire les systèmes d'indicateurs dans un cadre formel théorique ou analytique

5.3. Conclusions : vers une validation « sociale » des indicateurs environnementaux ?

Mon travail de thèse a proposé une validation d'un indicateur potentiel de biodiversité forestière et une réflexion sur ce processus. Les étapes abordées se rattachent à un certain nombre de critères de validation générale des indicateurs environnementaux et constitutent une première forme de standardisation – partielle – de ce processus : établissement de standards et quantification des biais probables, compréhension des facteurs d'influence dans une optique d'applicabilité à la gestion et quantification du lien avec l'*indicandum*. Même si des limites ont été mises en évidence et que les perspectives de recherche restent nombreuses, l'intérêt que portent les gestionnaires aux microhabitats grandit au fur et à mesure de l'acquisition d'une connaissance précise sur leur rôle et de leur dynamique. De ce fait et malgré les limites inhérentes aux indicateurs indirects (structuraux), on peut constater une forme de validation par l'usage de leur potentiel à indiquer la biodiversité. Au-delà de ce constat, il serait d'ailleurs intéressant de mieux comprendre les raisons et mécanismes sociaux de cet intérêt.

Ainsi, le processus de validation d'un indicateur environnemental a de multiples facettes qui n'impliquent pas uniquement des disciplines issues de l'écologie, ni même des chercheurs. Au cours de mon travail, j'ai essentiellement traité de la validation d'un indicateur potentiel de description scientifique de la biodiversité (au sens de Heink & Kowarik, 2010b). Cette thèse a apporté des avancées méthodologiques ainsi qu'un début de contextualisation de l'indicateur et a insisté sur la mise en évidence d'un lien entre microhabitats et la biodiversité de trois groupes taxonomiques. Cette approche est typique de la validation scientifique (par opposition à une validation politique) d'un indicateur de biodiversité, pour laquelle la mise en évidence d'une corrélation entre indicateur et indicandum revêt une importance primordiale (Heink & Kowarik, 2010b). Pourtant, un processus de validation, lorsqu'il est vu au travers d'un prisme disciplinaire élargi (notamment par les sciences politiques), ne se limite pas à la simple mise en évidence de ce lien, qui n'est d'ailleurs qu'un critère parmi d'autres dans un processus politique (Heilmeier et al., 2000; Niemeijer & de Groot, 2008). Ici, le Tableau 23 est une tentative pour aller plus loin sur ce processus dans le cas des microhabitats. Il montre qu'une partie des critères de validation mis en avant par Niemeijer and de Groot (2008) peut être complétée grâce à une approche à la fois analytique (corrélative) et discursive, mais qui demeure partielle. En particulier, certains critères relevant des dimensions politique et de gestion ne sont pas ou peu traités dans ce travail de thèse. Ils mettent en évidence une approche restrictive du travail de validation des indicateurs par les écologues, et montrent, comme dans de nombreux autres cas, le potentiel peu exploité de collaboration interdisciplinaire autour des indicateurs (Heink & Kowarik, 2010b).

Ainsi, s'il semble toujours crucial que les scientifiques éclairent les décisions politiques, il est également important de bien différencier le processus de recherche du processus politique : les méthodes et les hypothèses scientifiques, du fait de leur exigence d'objectivité, ne doivent pas subir d'influence politique ; réciproquement, la décision politique doit s'affranchir de normes implicitement définies par les scientifiques (*e.g.* Rametsteiner et al., 2011), à travers, par exemple, un usage ambigu d'indicateurs de biodiversité (Angelstam et al., 2013; Heink & Kowarik, 2010b; Turnhout et al., 2007). En particulier, l'acceptation et la compréhension des indicateurs de biodiversité sont pointés comme des éléments absents de la littérature scientifique sur le sujet (Heink & Kowarik, 2010b). Pourtant, parce que ce sont des objets frontières qui assurent la communication entre des mondes aux standards différents (scientifiques, politiques, gestionnaires, public, Turnhout, 2009), la construction et la validation d'indicateurs par des scientifiques ne devrait pas s'affranchir – même involontairement – de l'apport d'autres disciplines.

Le cas des microhabitats est malgré tout intermédiaire car, s'il ne bénéficie pas pour le moment d'un apport interdisciplinaire fort (en dehors de la mobilisation de connaissances en biologie, en écologie et en foresterie), l'adoption par les gestionnaires forestiers et de milieux naturels ainsi que leur demande de standardisation portée par l'Institut Forestier Européen (Kraus et al., 2016) témoigne

d’une co-construction effective – à l’instar du bois mort (Deuffic, 2010; Deuffic & Lyser, 2012). La large diffusion du catalogue initialement produit par l’Institut Forestier Européen (Kraus et al., 2016) et sa traduction dans de nombreuses langues peuvent être assimilées à une forme de validation sociale – ou tout au moins gestionnaire – de cet indicateur. Par contre, malgré un certain nombre de critères qui contribuent à leur validation en tant qu’indicateurs écologiques, il n’est pas pour le moment évident qu’ils soient de bons candidats au statut d’indicateurs de politique forestière (au sens de Heink & Kowarik, 2010b) ni même qu’ils aient cette vocation. De nombreux verrous, à la fois scientifiques, politiques et de gestion, restent à lever.

Bibliographie

Ahrends, A., Rahbek, C., Bulling, M.T., Burgess, N.D., Platts, P.J., Lovett, J.C., Kindemba, V.W., Owen, N., Sallu, A.N., Marshall, A.R., Mhoro, B.E., Fanning, E. & Marchant, R. (2011) Conservation and the botanist effect. *Biological Conservation*, **144**, 131-40.

Allegrini, M.C., Canullo, R. & Campetella, G. (2009) ICP-Forests (International Co-operative programme on assessment and monitoring of Air pollution effects on forests): Quality assurance procedure in plant diversity monitoring. *Journal of Environmental Monitoring*, **11**, 782-87.

Angelstam, P., Roberge, J.M., Axelsson, R., Elbakidze, M., Bergman, K.O., Dahlberg, A., Degerman, E., Eggers, S., Esseen, P.A., Hjalten, J., Johansson, T., Muller, J., Paltto, H., Snall, T., Soloviy, I. & Tornblom, J. (2013) Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: the Swedish Forest Stewardship Council standard as a case study. *Ambio*, **42**, 229-40.

Archaux, F., Gosselin, F., Bergès, L. & Chevalier, R. (2006) Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. *Journal of Vegetation Science*, **17**, 299-306.

Barbier, S., Chevalier, R., Loussot, P., Bergès, L. & Gosselin, F. (2009) Improving biodiversity indicators of sustainable forest management: Tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. *Forest Ecology and Management*, **258**, S176-S86.

Bauhus, J., Puettmann, K. & Messier, C. (2009) Silviculture for old-growth attributes. *Forest Ecology and Management*, **258**, 525-37.

Becker, W., Saisana, M., Paruolo, P. & Vandecasteele, I. (2017) Weights and importance in composite indicators: Closing the gap. *Ecological Indicators*, **80**, 12-22.

Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P. & Laudenslayer, W.F. (2005) *The afterlife of the tree* WWF Poland, Warszawa-Hajnowka.

Bockstaller, C. & Girardin, P. (2003) How to validate environmental indicators. *Agricultural Systems*, **76**, 639-53.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127-35.

Bouget, C. (2013) *Déterminants des communautés saproxyliques en forêt tempérée : applications au suivi et à la conservation de la biodiversité*. Habilitation à Diriger des Recherches, Univesité d'Orléans.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The FRench Information system on Saproxylic BEetle Ecology (FRISBEE): An ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie (La Terre et la Vie)*, **63**, 33-36.

Bouget, C., Larrieu, L. & Brin, A. (2014) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, **36**, 656-64.

Bouget, C., Larrieu, L., Nusillard, B. & Parmain, G. (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, **22**, 2111-30.

Bouleau, G. (2016) Pourquoi chercher la petite bête ? Les enjeux politiques de l'indice biotique en France (1964-1969). *VertigO*.

Bouleau, G., Deuffic, P., Sergent, A., Paillet, Y. & Gosselin, F. (2016) Entre logique de production et de préservation : l'évolution de l'information environnementale dans les domaines de l'eau et de la forêt. *VertigO*, **16**.

Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O. & Gosselin, F. (2016) Effects of forest structure, management and landscape on bird and bat communities. *Environmental Conservation*, 1-13.

Bruciamacchie, M. (2005). Protocole de suivi d'espaces naturels protégés. In, p 42. ENGREF - MEDD.

Bull, E.L., Parks, C.G. & Torgersen, T.R. (1997). Trees and logs important to wildlife in the interior Columbia river basin. In, p 55. Pacific Northwest Research Station, USDA Forest Service, Portland USA.

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.C. & Watson, R. (2010) Global biodiversity: Indicators of recent declines. *Science*, **328**, 1164-68.

Chen, G., Kéry, M., Zhang, J. & Ma, K. (2009) Factors affecting detection probability in plant distribution studies. *Journal of Ecology*, **97**, 1383-89.

Chisholm, R.A., Lim, F., Yeoh, Y.S., Seah, W.W., Condit, R. & Rosindell, J. (2018) Species-area relationships and biodiversity loss in fragmented landscapes. *Ecology Letters*, **21**, 804-13.

Clark, J.S. (2005) Why environmental scientists are becoming Bayesians? *Ecology Letters*, **8**, 2-14.

Cockle, K.L., Martin, K. & Drever, M.C. (2010) Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation*, **143**, 2851-57.

Cockle, K.L., Martin, K. & Wesołowski, T. (2011) Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment*, **9**, 377-82.

Commarmot, B., Brändli, U.-B., Hamor, F. & Lavnyy, V. (2013) *Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure* Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf; Ukrainian National Forestry University, L'viv; Carpathian Biosphere Reserve, Rakhiv.

Connor, E.F. & McCoy, E.D. (2001) Species-area relationships. *Encyclopedia of Biodiversity*, **5**, 397-411.

Convention on Biological Diversity. (1992). Convention on Biological Diversity. In, p 83. Secretariat of the Convention on Biological Diversity (CBD). United Nations Environment Programme.

Courbaud, B., Pupin, C., Letort, A., Cabanettes, A., Larrieu, L. & Börger, L. (2017) Modelling the probability of microhabitat formation on trees using cross-sectional data. *Methods in Ecology and Evolution*, **8**, 1347-59.

Dajoz, R. (2007) *Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier* Tec & Doc Lavoisier, Paris.

Dale, V.H. & Beyeler, S.C. (2001) Challenges in the development and use of ecological indicators. *Ecological Indicators*, **1**, 3-10.

De Cáceres, M. & Legendre, P. (2009) Associations between species and groups of sites: Indices and statistical inference. *Ecology*, **90**, 3566-74.

Delbaere, B. (2004) European Policy Review: Starting to Achieve the 2010 Biodiversity Target. *Journal for Nature Conservation*, **12**, 141-42.

Deuffic, P. (2010) Dead wood for biodiversity - Foresters torm between mistrust and commitment. *Revue Forestière Française*, **62**, 71-85.

Deuffic, P. & Lyser, S. (2012) Biodiversity or bioenergy: Is deadwood conservation an environmental issue for French forest owners? *Canadian Journal of Forest Research*, **42**, 1491-502.

EEA. (1999). Environmental indicators: typology and overview. In *Technical Report no 25*. European Environment Agency, Copenhagen.

Elton, C. (1927) *Animal Ecology* Sidgwick and Jackson, London.

Fahrig, L. (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649-63.

Feest, A. (2013) The utility of the Streamlining European Biodiversity Indicators 2010 (SEBI 2010). *Ecological Indicators*, **28**, 16-21.

Ferretti, M. (2013). A quality assurance framework for designing forest monitoring programs. In *Forest monitoring. Methods for terrestrial investigation in Europe with an overview of North America and Asia* (eds M. Ferretti & A. Fischer), Vol. 12, pp. 77-90. Elsevier.

Ferris, R. & Humphrey, J.W. (1999) A review of potential biodiversity indicators for application in British forests. *Forestry*, **72**, 313-28.

Finn, J.A. (2001) Ephemeral resource patches as model systems for diversity-function experiments. *Oikos*, **92**, 363-66.

Forest Europe. (2015a). State of Europe's Forests 2015. In.

Forest Europe. (2015b). Updating of the pan-European Indicators for Sustainable Forest Management. In *Workshop on the updating of the pan-European Indicators for Sustainable Forest Management, 27-29 April 2015*, p 30. Forest Europe, Madrid, Spain.

Forman, R.T.T. & Godron, M. (1986) *Landscape ecology* Wiley, New York.

Gabrielsen, P. & Bosch, P. (2003). Environmental Indicators: Typology and Use in Reporting. In *EEA internal working paper*, p 20. European Environment Agency.

Gao, T., Nielsen, A.B. & Hedblom, M. (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, **57**, 420-34.

Gosselin, F. (2011) *Propositions pour améliorer l'équipement biométrique du détective écologique: application à la modélisation de la relation entre gestion forestière et biodiversité*. Habilitation à Diriger des Recherches, Université Pierre et Marie Curie.

Gosselin, F., Gosselin, M. & Paillet, Y. (2012) Suivre l'état de la biodiversité forestière : pourquoi ? comment ? *Revue Forestière Française*, **LXIV**, 683-700.

Gossner, M.M., Lade, P., Rohland, A., Sichardt, N., Kahl, T., Bauhus, J., Weisser, W.W. & Petermann, J.S. (2016) Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry. *Journal of Animal Ecology*, **85**, 213-26.

Gouix, N. & Brustel, H. (2012) Emergence trap, a new method to survey Limoniscus violaceus (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation*, **21**, 421-36.

Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk*, **34**, 427–33.

Großmann, J., Schultze, J., Bauhus, J. & Pyttel, P. (2018) Predictors of Microhabitat Frequency and Diversity in Mixed Mountain Forests in South-Western Germany. *Forests*, **9**, 104.

Halsey, L.G., Curran-Everett, D., Vowler, S.L. & Drummond, G.B. (2015) The fickle P value generates irreproducible results. *Nature Methods*, **12**, 179-85.

Hammond, A., Adriaanse, A., Rodenburg, E., Bryant, D. & Woodward, R. (1995). Environmental indicators: a systematic approach to measuring and reporting on environmental policy performance in the context of sustainable development. In *Environmental indicators: a systematic approach to measuring and reporting on environmental policy performance in the context of sustainable development*.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666-73.

Heilmeier, H., Baronius, K., Kuhn, A.J. & Nebe, W. (2000) Biomass and nutrient relationships of Betula pendula, Fagus sylvatica, Picea abies and Abies alba with varying nitrogen and sulphur additions in a pot experiment. *Forstwissenschaftliches Centralblatt*, **119**, 161-76.

Heink, U. & Kowarik, I. (2010a) What are indicators? On the definition of indicators in ecology and environmental planning. *Ecological Indicators*, **10**, 584-93.

Heink, U. & Kowarik, I. (2010b) What criteria should be used to select biodiversity indicators? *Biodiversity and Conservation*, **19**, 3769-97.

Herrault, P.A., Larrieu, L., Cordier, S., Gimmi, U., Lachat, T., Ouin, A., Sarthou, J.P. & Sheeren, D. (2016) Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae). *Landscape Ecology*, **31**, 877-93.

Herrmann, S., Dabbert, S. & Schwarz-von Raumer, H.-G. (2003) Threshold values for nature protection areas as indicators for bio-diversity—a regional evaluation of economic and ecological consequences. *Agriculture, Ecosystems & Environment*, **98**, 493-506.

Hunter, M.L., Acuña, V., Bauer, D.M., Bell, K.P., Calhoun, A.J.K., Felipe-Lucia, M.R., Fitzsimons, J.A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C.J., Medellin, R.A., Nelson, E.J. & Poschlod, P. (2017) Conserving small natural features with large ecological roles: A synthetic overview. *Biological Conservation*, **211**, 88-95.

Hutchinson, G.E. (1957). Concluding remarks In *Cold Spring Harbor Symposia on Quantitative Biology*, Vol. 22, pp. 415-27.

Inhaizer, H., Wolfslehner, B., Baycheva, T., Lier, M. & Prins, K. (2013). Implementing Criteria and Indicators (C&I) for Sustainable Forest Management (SFM) in Europe. In, p 141. European Forest Institute.

Jiguet, F., Devictor, V., Julliard, R. & Couvet, D. (2012) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica*, **44**, 58-66.

Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larrieu, L., Nagel, T.A., Begovič, K., Čada, V., Diku, A., Frankovič, M., Janda, P., Kameniar, O., Keren, S., Kjučukov, P., Lábusová, J., Langbehn, T., Málek, J., Mikac, S., Morrissey, R.C., Nováková, M., Schurrman, J.S., Svobodová, K., Synek, M., Teodosiu, M., Toromani, E., Trotsiuk, V., Vítková, L. & Svoboda, M. (2018) Profiles of tree-related microhabitats in European primary beech-dominated forests. *Forest Ecology and Management*, **429**, 363-74.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A. & Winter, S. (2016). Catalogue of tree microhabitats – Reference field list. In. Integrate+ Technical Paper, European Forest Insitute, Freiburg, Germany.

Kraus, D., Schuck, A., Bebi, P., Blaschke, M., Bütler, R., Flade, M., Heintz, W., Krumm, F., Lachat, T., Larrieu, L., Lehnerova, L., M., L., Mergner, U., Pach, M., Paillet, Y., Pyttel, P., T., R., Santopuoli, G., K., S., Sturm, K., Vandekerkhove, K., Winter, S. & Witz, M. (2017). *Spatially explicit database of tree related microhabitats (TreMs)*. GBIF.org. https://doi.org/10.15468/ocof3v

Laiolo, P., Rolando, A. & Valsania, V. (2004) Responses of birds to the natural re-establishment of wilderness in montane beechwoods of North-western Italy. *Acta Oecologica*, **25**, 129-36.

Lamb, E.G. , Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J. & Haughland, D.L. (2009) Indices for monitoring biodiversity change: Are some more effective than others? *Ecological Indicators*, **9**, 432-44.

Larjavaara, M. & Muller-Landau, H.C. (2013) Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, **4**, 793-801.

Larrieu, L. (2014) *Les dendro-microhabitats : facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique*, Institut National Polytechnique de Toulouse, Toulouse, France.

Larrieu, L. & Cabanettes, A. (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Canadian Journal of Forest Research*, **42**, 1433-45.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C. & Deconchat, M. (2014a) Tree microhabitats at the stand scale in montane beech-fir forests: Practical information for taxa conservation in forestry. *European Journal of Forest Research*, **133**, 355-67.

Larrieu, L., Cabanettes, A. & Delarue, A. (2012) Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *European Journal of Forest Research*, **131**, 773-86.

Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C. & Deconchat, M. (2014b) Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring. *Forest Ecology and Management*, **334**, 163-73.

Larrieu, L., Cabanettes, A. & Sarthou, J.P. (2015) Hoverfly (Diptera: Syrphidae) richness and abundance vary with forest stand heterogeneity: Preliminary evidence from a montane beech fir forest. *European Journal of Entomology*, **112**, 755-69.

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B. & Vandekerkhove, K. (2018) Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecological Indicators*, **84**, 194-207.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **11**, 1027-39.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015) Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation*, **191**, 558-66.

Lee, W., McGlone, M. & Wright, E. (2005). A review of national and international systems and a proposed framework for future biodiversity monitoring by the Department of Conservation. In, p 218. Landcare Research, Wellington, New Zealand.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomology Society of America*, **71**, 237-40.

Levrel, H., Loïs, G. & Couvet, D. (2007) Indicateurs de biodiversité pour les forêts françaises. état des lieux et perspectives. *Revue Forestière Française*, **59**, 45-56.

Lier, M., Parviainen, J., Nivet, C., Gosselin, M., Gosselin, F. & Paillet, Y. (2013). The use of European criteria and indicator systems for measuring changes in forest biodiversity. In *Integrative approaches as an opportunity for the conservation of forest biodiversity* (eds D. Kraus & F. Krumm), pp. 32-42. European Forest Institute, Freiburg, DEU.

Lindenmayer, D.B., Blanchard, W., Blair, D., McBurney, L. & Banks, S.C. (2017) Relationships between tree size and occupancy by cavity-dependent arboreal marsupials. *Forest Ecology and Management*, **391**, 221-29.

Lindenmayer, D.B., Franklin, J.F. & Fischer, J. (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, **131**, 433-45.

Lindenmayer, D.B., Margules, C.R. & Botkin, D.B. (2000) Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*, **14**, 941-50.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R. & Gibbons, P. (2009) Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation*, **142**, 33-42.

Lombardi, F., Marchetti, M., Corona, P., Merlini, P., Chirici, G., Tognetti, R., Burrascano, S., Alivernini, A. & Puletti, N. (2015) Quantifying the effect of sampling plot size on the estimation of structural indicators in old-growth forest stands. *Forest Ecology and Management*, **346**, 89-97.

Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. & Callaway, R.M. (2004) Rethinking plant community theory. *Oikos*, **107**, 433-38.

MacArthur, R.H. & Wilson, E.O. (1967). The Theory of Island Biogeography. In *Princeton University Press (Princeton, NJ).*

Maciejewski, L., Lepareur, F., Viry, D., Bensettiti, F., Puissauve, R. & Touroult, J. (2016) État de conservation des habitats : propositions de définitions et de concepts pour l'évaluation à l'échelle d'un site Natura 2000. *Revue d'Ecologie (La Terre et la Vie)*, **71**, 3-20.

Maris, B. (2003) *Antimanuel d'économie : Tome 1, les fourmis*.

Martin, K., Aitken, K.E.H. & Wiebe, K.L. (2004) Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *Condor*, **106**, 5-19.

Martin, K. & Eadie, J.M. (1999) Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management*, **115**, 243-57.

Michel, A.K. & Winter, S. (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *Forest Ecology and Management*, **257**, 1453-64.

Miklín, J., Sebek, P., Hauck, D., Konvicka, O. & Cizek, L. (2018) Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles. *Diversity and Distributions*, **24**, 208-18.

Moriarty, P.E., Hodgson, E.E., Froehlich, H.E., Hennessey, S.M., Marshall, K.N., Oken, K.L., Siple, M.C., Ko, S., Koehn, L.E., Pierce, B.D. & Stawitz, C.C. (2018) The need for validation of ecological indices. *Ecological Indicators*, **84**, 546-52.

Müller, J. & Bütler, R. (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, **129**, 981-92.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-42.

Niemeijer, D. & de Groot, R.S. (2008) A conceptual framework for selecting environmental indicator sets. *Ecological Indicators*, **8**, 14-25.

Niemela, J. (2000) Biodiversity monitoring for decision-making. *Annales Zoologici Fennici*, **37**, 307-17.

Noss, R.F. (1990) Indicators for monitoring biodiversity - A hierarchical approach. *Conservation Biology*, **4**, 355-64.

OECD. (1994). Environmental Indicators – OECD Core Set. In. OECD, Paris.

Ovaskainen, O. (2002) Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, **218**, 419-33.

Pacifici, K., Simons, T.R. & Pollock, K.H. (2008) Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk*, **125**, 600-07.

Paillet, Y. (2017) Suivis nationaux de biodiversité en forêt : une lecture au travers des variables essentielles de biodiversité. *Naturae*, **6**, 1-11.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F. & Guilbert, E. (2017) Snags and large trees drive higher tree microhabitat densities in strict forest reserves. *Forest Ecology and Management*, **389**, 176-86.

Paillet, Y., Archaux, F., du Puy, S., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F. & Guilbert, E. (in press) The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*, 1-13.

Paillet, Y., Bergès, L., Hjälten, J., Odor, P., Avon, C., Bernhardt-Romermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010) Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conservation Biology*, **24**, 101-12.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F. & Gosselin, F. (2015a) Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. *Ecological Indicators*, **49**, 14-23.

Paillet, Y., Debaive, N., Archaux, F., Boulanger, V., Gilg, O. & Guilbert, E. (preprint) Nothing else matters? A nationwide study of microhabitat drivers at the tree scale. *bioRxiv*, **335836**.

Paillet, Y., Parviainen, J., Gosselin, M., Gosselin, F. & Lier, M. (2013). Monitoring forest biodiversity in Europe: state of the art, challenges and opportunities. In *Integrative approaches as an opportunity fir the conservation of forest biodiversity* (eds D. Kraus & F. Krumm), pp. 242-52. European Forest Institute, Freiburg, DEU.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O. & Gosselin, F. (2015b) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management*, **346**, 51-64.

Parks, C.G., Bull, E.L. & Torgersen, T.R. (1997). Field guide for the identification of snags and logs in the interior Columbia River basin. In *General Technical Report - Pacific Northwest Research Station, USDA Forest Service*, p 41.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652-61.

Rametsteiner, E., Pülzl, H., Alkan-Olsson, J. & Frederiksen, P. (2011) Sustainability indicator development—Science or political negotiation? *Ecological Indicators*, **11**, 61-70.

Ranius, T. (2002) Osmoderma eremita as an indicator of species richness of beetles in tree hollows. *Biodiversity and Conservation*, **11**, 931-41.

Ranius, T., Johansson, V. & Fahrig, L. (2011) Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. *Biodiversity and Conservation*, **20**, 2027-40.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F. & Kerbiriou, C. (2013a) Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecological Indicators*, **34**, 221-30.

Regnery, B., Paillet, Y., Couvet, D. & Kerbiriou, C. (2013b) Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? *Forest Ecology and Management*, **295**, 118-25.

Remm, J. & Lõhmus, A. (2011) Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*, **262**, 579-85.

Rendigs, A., Radespiel, U., Wrogemann, D. & Zimmermann, E. (2003) Relationship between microhabitat structure and distribution of mouse lemurs (Microcebus spp.) in Northwestern Madagascar. *International Journal of Primatology*, **24**, 47-64.

Roberge, J.-M. & Angelstam, P. (2004) Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conservation Biology*, **18**, 76-85.

Roberge, J.M. & Angelstam, P. (2006) Indicator species among resident forest birds - A cross-regional evaluation in northern Europe. *Biological Conservation*, **130**, 134-47.

Robles, H. & Martin, K. (2014) Habitat-mediated variation in the importance of ecosystem engineers for secondary cavity nesters in a nest web. *PLoS ONE*, **9**.

Rykiel, E.J. (1996) Testing ecological models: the meaning of validation. *Ecological Modelling*, **90**, 229-44.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T. & Essl, F. (2018) Where are Europe's last primary forests? *Diversity and Distributions*.

Samhouri, J.F., Levin, P.S. & Ainsworth, C.H. (2010) Identifying thresholds for ecosystem-based management. *PLoS ONE*, **5**.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C. & Mori, A. (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, **55**, 267-78.

Scholes, R.J., Mace, G.M., Turner, W., Geller, G.N., Jürgens, N., Larigauderie, A., Muchoney, D., Walther, B.A. & Mooney, H.A. (2008) Ecology: Toward a global biodiversity observing system. *Science*, **321**, 1044-45.

Scholes, R.J., Walters, M., Turak, E., Saarenmaa, H., Heip, C.H.R., Tuama, É.Ó., Faith, D.P., Mooney, H.A., Ferrier, S., Jongman, R.H.G., Harrison, I.J., Yahara, T., Pereira, H.M., Larigauderie, A. & Geller, G. (2012) Building a global observing system for biodiversity. *Current Opinion in Environmental Sustainability*, **4**, 139-46.

Secretariat of the Convention on Biological Diversity. (2006). Global Biodiversity Outlook 2. In, p 81. Convention on Biological Diversity (CBD), Montreal.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J. & Baraloto, C. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, **53**, 934-43.

Siitonen, J. (2012). Microhabitats. In *Biodiversity in dead wood* (eds J.N. Stokland, J. Siitonen & B.G. Jonsson), pp. 150-82. Cambridge University Press, New York, USA.

Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Kelly, T., Iremonger, S., McKee, A.M. & Giller, P. (2008) Identifying practical indicators of biodiversity for stand-level management of plantation forests. *Biodiversity and Conservation*, **17**, 991-1015.

Speight, M.C.D., Castella, E. & Sarthou, J.P. (2013). StN 2013. In *Syrph the Net on CD, Issue 9. The database of European Syrphidae* (eds M.C.D. Speight, E. Castella, J.-P. Sarthou & C. Vanappelghem). Syrph the Net Publications, Dublin.

Star, S.L. & Griesemer, J.R. (1989) Institutional Ecology, 'Translations' and Boundary Objects: Amateurs and Professionals in Berkeley's Museum of Vertebrate Zoology, 1907–39. *Social Studies of Science*, **19**, 387-420.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305-08.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, **31**, 79-92.

Tillon, L. & Aulagnier, S. (2014) Tree cavities used as bat roosts in a European temperate lowland sub-Atlantic forest. *Acta Chiropterologica*, **16**, 359-68.

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D., Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Höft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, J., Lojenga, R.K., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., Van Kolck, J., Visconti, P. & Ye, Y. (2014) A mid-term analysis of progress toward international biodiversity targets. *Science*, **346**, 241-44.

Tomppo, E., Gschwantner, T., Lawrence, M. & Mc Roberts, R.E. (2010) *National forest inventories. Pathways for common reporting* Springer Science, Heidelberg, Allemagne.

Trompette, P. & Vinck, D. (2009) Retour sur la notion d'objet-frontière. *Revue d'anthropologie des connaissances*, **3, 1**, 5.

Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology, Evolution, and Systematics*, **20**, 171-97.

Turnhout, E. (2009) The effectiveness of boundary objects: The case of ecological indicators. *Science and Public Policy*, **36**, 403-12.

Turnhout, E., Hisschemöller, M. & Eijsackers, H. (2007) Ecological indicators: Between the two fires of science and policy. *Ecological Indicators*, **7**, 215-28.

UNEP. (1997). Global Environment Outlook In. United Nations Environment Programme, Nairobi.

UNEP. (2007). GEO4: Global Environment Outlook - Environment for Development. In. United Nations Environment Programme, Nairobi.

Vačkář, D., Ten Brink, B., Loh, J., Baillie, J.E.M. & Reyers, B. (2012) Review of multispecies indices for monitoring human impacts on biodiversity. *Ecological Indicators*, **17**, 58-67.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde, P. (2009) When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *Forest Ecology and Management*, **258**, 425-35.

Vuidot, A., Paillet, Y., Archaux, F. & Gosselin, F. (2011) Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, **144**, 441-50.

Wesołowski, T., Mitrus, C., Czeszczewik, D. & Rowiński, P. (2010) Breeding bird dynamics in a primeval temperate forest over thirty-five years: Variation and stability in the changing world. *Acta Ornithologica*, **45**, 209-32.

Winter, S., Höfler, J., Michel, A.K., Böck, A. & Ankerst, D.P. (2015) Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. *European Journal of Forest Research*, **134**, 335-47.

Winter, S. & Möller, G.C. (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management*, **255**, 1251-61.

Wolfslehner, B. (2007) *The use of indicators models for the evaluation of sustainable forest management in a multi-criteria analysis framework*, University of natural Ressources and Applied Life Sciences, Vienna, Austria.

Wright, D.H. (1983) Species-Energy Theory: An Extension of Species-Area Theory. *Oikos*, **41**, 496-506.

Zilliox, C. & Gosselin, F. (2014) Tree species diversity and abundance as indicators of understory diversity in French mountain forests: Variations of the relationship in geographical and ecological space. *Forest Ecology and Management*, **321**, 105-16.

Annexes A : Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization – Supplementary materials

Laurent Larrieu, Yoan Paillet, Susanne Winter, Rita Bütler, Daniel Kraus, Frank Krumm, Thibault Lachat, Alexa K. Michel, Baptiste Regnery, Kris Vandekerkhove

Ecological Indicators 84 (2018) 176-186

Annexe 1 : Literature used to build Tableau 4; experts consulted: Gilles Corriol (fungi & lichens), Maria Infante-Sanchez (bryophytes), Christophe Bouget (invertebrates), Luc Barbaro (vertebrates)

Arthropods and other invertebrates

Alexander, K., 2002. The invertebrates of living and decaying timber in Britain and Ireland— a provisional annotated checklist. English Nature Research Reports No. 467. Department for Environment, Food and Rural Affairs and English Nature, Cranfield University at Silsoe, Bedfordshire, U.K.

Alexander, K.N., 2008. Tree Biology and Saproxylic Coleoptera: Issues of Definitions and Conservation Language. Revue D'Ecologie la Terre et la Vie, 9-13.

Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P., Laudenlayer, W.F. (eds), 2005. The afterlife of a tree. WWF Poland, Warszawa-Hajnowka.

Bayliss Elliott, J.S., 1914. Fungi in the nests of ants: Plate II. Transactions of the British Mycological Society 5, 138-IN2.

Belmain SR, Simmonds MSJ, Blaney WM, 2002. Influence of odor from wood-decaying fungi on host selection behavior of deathwatch beetle, Xestobium rufovillosum. Journal of Chemical Ecology 28(4), 741-754.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management 261, 211-220.

Bouget C, Parmain G, Gilg O, Noblecourt T, Nusillard B, Paillet Y, Pernot C, Larrieu L, Gosselin F, 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Animal Conservation 17 (4), 342-353.

Branco, M., Santos, M., Calvao, T., Telfer, G., Paiva, M.R., 2008. Arthropod diversity sheltered in Thaumetopoea pityocampa (Lepidoptera: Notodontidae) larval nests. Insect Conserv Divers 1, 215-221.

Castella, G., Chapuisat, M., Christe, P., 2008a. Prophylaxis with resin in wood ants. Animal Behaviour 75, 1591-1596.

Castella, G., Chapuisat, M., Moret, Y., Christe, P. 2008b. The presence of conifer resin decreases the use of the immune system in wood ants. Ecological Entomology 33, 408–412.

Chandler, P., 2001. The Flat-footed flies (diptera : Opetiidae and Platypezidae) of Europe. Leiden, Boston, Köln: Brill.

Chapuisat, M., Opplinger, A., Magliano, P., Christe, P., 2007. Wood ants use resin to protect themselves against pathogens. Proceedings of the Royal Society B 274, 2013-2017.

Crowson, R.A., 1981. The biology of the Coleoptera. London: Academic Press. Dublin, Ireland.

Dajoz, R., 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier, 2ème édn. Tec et Doc Lavoisier, Paris.

Germain L., 1930. Faune de France 21: Mollusques terrestres et fluviatiles. FFSSN, Paris, 480p.Géroudet P., 1980. Les passereaux d'Europe. Delachaux et Niestlé, Neuchâtel.

Gerson, U., Seaward, M.R.D., 1977. Lichen-invertebrate associations. In: Lichen Ecology, MRD Seaward, ed. Pp 69-119. Academic Press, London.

Gouix N., 2012. Gestion forestière et Biodiversité, les enjeux de conservation d'une espèce parapluie; *Limoniscus violaceus* (Coleoptera). Thèse de doctorat. UPCM.

Hanski, I., 2005. The shrinking world: Ecological consequences of habitat loss. Excellence in Ecology 14. IEI, Germany.

Heiss, E., Pericart, J., 2007. Hemiptères Aradidae Piesmatidae et Dipsocoromorphes euro-méditerranéens. Faune de France (France et régions limitrophes) 91. Fédération Française des sociétés de sciences naturelles.

Hjältén, J., Atlegrim, O., Sandström, F., Pettersson, R., Rexstad, E.A., 2006. Occurrence of flat bugs (Heteroptera: Aradidae) in burned and unburned forests. Entomologica Fennica 17, 130-135.

Johanson, T., Olson, J., Hjalten, J., Jonson, B.G., Ericson, L., 2006. Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden, Forest Ecology and Management 237, 335-341.

Jonsell, M., Nordlander, G., Ehnström, B., 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. Ecological Bulletins 49, 173-194.

Kitching, R. L., 1983. Community structure in water-filled tree-holes in Europe and Australia -some comparisons and speculations. In Frank, J. H. & L. P. Lounibos (eds), Phytotelmata: Terrestrial Plants as Hosts of Aquatic Insect Communities. Plexus Press, Medford, 205–222.

Lapeva-Gjonova, A., 2013. Ant-associated beetle fauna in Bulgaria: A review and new data. Psyche, ID 242037, 14 p.

Matthewman WG. & Pielou DP., 1971. Arthopods inhabiting the sporophores of Fomes fomentarius (Polyporacea) in Gatineau park, Quebec. Canadian Entomologist 103, 775-847.

Midgaard, F., Rukke, B.A., Sverdrup-Thygeson, A., 1998. Habitat use of the fungivorous beetle Bolitophagus reticulatus (Coleoptera : Tenebrionidae) : effects of basidiocarp size, humidity and competitors. Europaen Journal of Entomology 95, 559-570.

Möller, G., 1991. Warum und wie sollen Holzbiotope geschützt werden? In: Auhagen, A., Platen, R., Sukopp, H. (Hrsg.): Rote Listen der Pflanzen und Tiere in Berlin, TU-Berlin, 421-437.

Möller, G.C., 2005. Habitatstrukturen holzbewohnender Insekten und Pilze (Habitat structures of saproxylic beetles and fungi), LÖBF-Mitteilungen 3, 30-35.

Möller, G., 2009. Struktur- und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera – Käfer. Diss. Freie Univ. Berlin.

Nikitski, N.B., Schigel, D.S., 2004. Beetles in polypores of the Moscow region: checklist and ecological notes. Entomologica Fennica 15, 6-22.

Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103, 85-91.

Rawlins, J.E., 1984. Mycophagy in Lepidoptera. In : Wheeler Q. & Blackwell M. (eds.). Fungus-Insect Relationships : perpestives in Ecology and Evolution. New York, Columbia University press, 382-423.

Ricarte, A., Jover, T., Marcos-García, M.A., Micó, E., Brustel, H., 2009. Saproxylic beetles (Coleoptera) and hoverflies (Diptera: Syrphidae) from a Mediterranean forest: towards a better understanding of their biology for species conservation, Journal of Natural History 43 (9), 583-607.

Rydkvist, T., Kraus, D., 2010. Prescribed burning for nature conservation in Västernorrland, Sweden. In: Montiel, C., Kraus, D. eds, 2010. Best practices of fire use – prescribed burning and suppression fire programmes in selected case-study regions in Europe EFI Research Report 24.

Schaffrath, U., 2003. Zu Lebensweise, Verbreitung und Gefährdung von Osmoderma eremita (Scopoli, 1763) (Coleoptera: Scarabaeoidea, Cetoniidae, Trichiinae). Teil 2. Philippia – Abhandlungen und Berichte aus dem Naturkundemuseum im Ottoneum zu Kassel, 249-336.

Schmidl, J., Sulzer, P., Kitching, R.L., 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia 598: 285-303.

Schwenke, W., 1978. Die Forstschädlinge Europas. Band 3: Schmetterlinge. Blackwell Verlag, Hamburg und Berlin.

Sevcik, J., 2006. Diptera associated with fungi in the Czech and Slovak republics. Casopis Slezkého Muzea Opava, 55, (Suppl. 2), 1-84.

Shaw, D.C., Watson,D.M., Mathiasen,R.L., 2004. Comparison of dwarf mistletoes (Arceuthobium spp., Viscaceae) in the western United States with mistletoes (Amyema spp., Loranthaceae) in Australia - ecological analogs and reciprocal models for ecosystem management. Australian Journal of Botany 52, 481-498.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am Nat 152, 510–529.

Stephenson, S.L., Wheeler, Q.D., McHugh, J.V., Fraissinet, P.R., 1994. New North American associations of Coleoptera with Myxomycetes. Journal of Natural History 28, 921-936.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge.

Vaillant, F., 1978. Les Systenus et leur habitat dendrotelme. Bull Société Ent Fr 83, 73-85.

Varga, I., Keresztes, B., Poczai, P., 2012. Data to the Hungarian insect fauna of European mistletoe (Viscum album). Novenyvedelem 48, 153-164.

Wheeler, Q., Miller, K.B., 2005. Slime-mold beetles of the genus Agathidium Panzer in North and Central America. Part I. Coleoptera: Leiodidae. Bulletin of the American Museum of Natural History, 290, 1-95.

Wheeler, Q., 1984. Evolution of slime mold feeding in leiodid beetles. In Wheeler Q. & Blackwell M. (eds.). Fungus-Insect Relationships: perpectives in Ecology and Evolution. New York, Columbia University press, 446-477.

Wikars, L.-O., 1997. Effects of forest fire and the ecology of fire-adapted insects. Comprehensive summaries of Uppsala dissertations, Acta Universitatis Upsaliensis 272.

Wikars, L.-O., 2002. Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6, 1-12.

Winter, S., 2005. Ermittlung von strukturellen Indikatoren zur Abschätzung des Einflusses forstlicher Bewirtschaftung auf die Biozönosen von Tiefland-Buchenwäldern. Determination of indicators for assessing the impact of silvicultural use on the biocoenosis of lowland beech forests in Germany. PhD thesis Technical University Dresden, 322 pp.

Winter, S., Möller, G.C., 2008, Microhabitats in lowland beech forests as a monitoring tool for nature conservation. Forest Ecology and Management 255, 1251-1261.

Winter, S., Begehold, H., Herrmann, M., Lüderitz, M., Möller, G., Rzanny, M., Flade ,M., 2015. Praxishandbuch - Naturschutz im Buchenwald. Land Brandenburg.

Yoshimoto, J., Kakutani, T., Nishida, T., 2005. Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecological Research 20, 405-414.

Yoshimoto, J., Nishida, T., 2007. Boring effect of carpenterworms (Lepidoptera : Cossidae) on sap exudation of the oak, *Quercus acutissima*. Applied Entomology and Zoology 42, 403-410.

Vertebrates

Arthur, L., Lemaire, M., 2009. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope, Mèze (coll. Parthénope). Muséum National d'Histoire naturelle. Paris.

Artois, 1989. Encyclopédie des carnivores de France. Le Renard roux (Vulpes vulpes L. 1758). SFEPM.

Banfield, A.W.F., 1974. The Mammals of Canada. National Museum of Canada, Ottawa.

Bauer, H.G., Fiedler, W., Bezzel, E., 2005. Das Kompendium der Vögel Mitteleuropas – Alles über biologie, Gefährdung und Schutz – Nonpasseriformes – Nichtsperlingsvögel. Aula-Verlag, Wiebelsheim.

Birks, J.D.S., Messenger, J.E., Halliwell, E.C. 2005. Diversity of den sites used by pine martens Martes martes: a response to the scarcity of arboreal cavities? Mammal Rev. 35 (3&4), 313-320.

Blondel, J., 2005. Bois mort et cavités: leur rôle pour l'avifaune cavicole. In: Vallauri, D. et al. (eds) Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, 137-142.

Boonman, M., 2000. Roost selection by noctules (Nyctalus noctula) and Daubenton's bats (Myotis daubentonii), Journal of Zoology 251, 385–389.

Bright, P.W., Morris, P.A., Michell-Jones, T. 2006. The dormouse conservation handbook, 2nd edition. External Relations Team, English Nature, Peterborough, UK.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and logs important to wildlife in the interior Columbia River basin. Gen. Tech. Rep. PNW-GTR-391. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Carlson, A., Sandstrom, U., Olsson, K., 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. Ardea 86(1), 109-119.

Carvalho, F., Carvalho, R., Mira, A., Beja, P., 2014. Use of tree hollows by a Mediterranean forest carnivore. Forest Ecology and Management 315, 54-62.

Cockle, K.L., Martin, K., Wesolowski, T., 2011. Woodpeckers, decay and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and Environment 9, 377-382.

Conner, D.A., 1983. Life in a rock pile. Natural History 6, 51-57.

Corbet, G., Ovenden, D., 1980. The mammals of Britain and Europe. William Collins Sons & Co Ltd.

Cramp, S. (chief editor) et al., 1980. Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Paleartic. Oxford University Press, New York.

Cramp S. (chief editor) et al., 1984. Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Paleartic. Volume I: Ostrich to Ducks. Oxford University Press. Oxford.

Cramp S. (chief editor) et al., 1989. Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Paleartic. Volume IV: Terns to Woodpeckers. Oxford University Press. Oxford.

Cramp S. (chief editor) et al. 1994. Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Paleartic. Volume VIII: Crows to Finches. Oxford University Press. Oxford.

Czeszczewik, D., Walankiewicz, W., Stańska, M., 2008. Small mammals in nests of cavity-nesting birds: Why should ornithologists study rodents ? Can. J. Zool. 86, 286-293.

Denison, W.C., 1973. Life in tall trees. Scientific American 228, 75-80.

Dietz, M., Frank, R., 1994. Beobachtungen zum Überwinterungsverhalten des Großen Abendseglers (Nyctalus noctula) im Philosophenwald in Gießen (Hessen). In: Current Problems of Bat Protection in Central and Eastern Europe, Symposium Bonn zitiert in Meschede, A., Heller, K.-G., 2000. Ökologie und Schutz von Fledermäusen in Wäldern. Schr.reihe Landschaftspfl. Naturschutz 66, 374 pp.

Duguet, R., Melki F. (eds.), 2003. Les Amphibiens de France, Belgique et Luxembourg. Collection Parthénope, éditions biotope, Mèze (France).

Edwards, R.Y, Ritcey, R.W., 1960. Foods of caribou in Wells Gray Park, British Columbia. The Canadian Field-Naturalist 74, 3-7.

Fernández, N., 1997. Reproducción del gato montés en el P. N. de Doñana. Galemys 9, 38-39.

Fernández N., Palomares, F. 2000. The selection of breeding dens by the endangered Iberian lynx (Lynx pardinus): implications for its conservation. Biological Conservation 94, 51-61.

Fox, J.L., Smith, C.A., 1988. Winter mountain goat diets in Southeast Alaska. Journal of Wildlife Management 52(2), 362-265.

Géroudet P., 1982. Les palmipèdes. Collection Les Beautés de la Nature. Delachaux et Niestlé, Neuchâtel.

Géroudet P., 1983. Limicoles, gangas et pigeons d'Europe. Collection Les Beautés de la Nature. Delachaux et Niestlé, Neuchâtel.

Géroudet P., 1984. Les rapaces diurnes et nocturnes d'Europe. Collection Les Beautés de la Nature. Delachaux et Niestlé, Neuchâtel.

Grindal, S.D.,1999. Habitat use by bats, Myotis spp., in western Newfoundland, Can. Field Nat. 113, 258-263.

Gunther, P.M., Horn, B.S., Babb, G.D., 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57, 32-44.

Harrison, C., 1977. Nids, œufs et poussins d'Europe. Bordas.

Jackson, J.A., Jackson, B.J.S., 2004. Ecological relationships between and woodpecker cavity sites. The Condor 106, 37-49.

Johnsson, K., Nilsson, S.G., Tjernberg, M., 1993. Characteristics and Utilization of Old Black Woodpecker Dryocopus-Martius Holes by Hole-Nesting Species. Ibis 135, 410-416.

Labrid, M., 1986. La Martre. Encyclopédie des carnivores de France, vol 9. SFEPM.

Le Louarn, H., Quéré, P.J., 2003. Les rongeurs de France - Faunistique et biologie; 2ème édition. INRA ed.

Libois R., 1991. La Fouine. Encyclopédie des carnivores de France, vol 10. SFEPM.

Livet, F., Roeder, J.J., 1987. La Genette. Encyclopédie des carnivores de France, vol 16. SFEPM.

Lovaty, F., 2012. Nidifications du Grimpereau des jardins Certhia brachydactyla dans des balais de sorcière sur pin maritime Pinus pinaster. Nos Oiseaux 59, 79-81.

Lovaty, F., 2014. L'importance du bois mort surpied et des microsites pour la reproduction de la mésange huppée Lophophanes cristatus : exemple dans une pinède de Pins maritimes Pinus pinaster de Charente-Maritime (France). Alauda 82, 3-18.

Lucan, R.K., Hanak, V., Horacek I, 2009. Long-term re-use of tree roosts by European forest bats. Forest Ecology and Management. 258, 1301-1306.

McClelland, B.R., Frissell, S.S., Fischer, W.C., Halvorson, C.H., 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. J. For. 77, 480–483.

Meschede, A., Heller, K.G., 2003. Ecologie et protection des chauves-souris en milieu forestier. Le Rhinolophe 16, 1-248.

Michel, A., Winter, S., 2009. Strukturvielfalt in Douglasienwäldern Nordamerikas und ihre Bedeutung für den Douglasienanbau in Deutschland. Eberswalder Forstliche Schriftenreihe 43, 23-27.

Noble, W.O., Meslow, C.E., Pope, M.D., 1990. Denning habits of black bears in the central Coast Range of Oregon. Report, Oregon State University, Corvallis, OR, 28 pp.

Olsson, O., 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. Doctoral thesis, Lund University, Department of Ecology, Lund.

Park, O., Auerbach, S., 1954. Further study of the tree-holes complex with emphasis on quantitative aspects of the fauna. Ecology, 35, 208-222.

Parks, C.G., Bull, E.L., Torgersen, T.R., 1997. Field guide for the identification of snags and logs in the Interior Columbia River Basin. USDA Forest Service General Technical Report, PNW-GTR-390, 40 pp.

Pénicaud, P., 2000. Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe 14: 37–68.

Psyllakis, J.M., Brigham, R.M., 2006. Characteristics of diurnal roosts used by female Myotis bats in sub-boreal forests, Forest Ecology and Management 223, 93–10.

Radu, S., 2005. La biodiversité du bois mort dans les forêts naturelles roumaines. In Vallauri et al. (coord.) Bois mort et à cavités – Une clé pour les forêts vivantes. Ed. Tec et Doc, Lavoisier.

Revilla, E., Palomares, F., Fernández, N. 2001. Characterisitcs, location and selection of diurnal resting dens by Eurasian badgers (Meles meles) in a low density area. J. Zool. 255, 291-299.

Richardson, D.H.S., Young, C.M., 1977. Lichens and vertebrates. In: Lichen Ecology, MRD Seaward, ed., 121-144. Academic Press, London.

Roberge, J.-M., Angelstram, P., Villard, M.-A., 2008. Specialized woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. Biological Conservation 141, 997-1012.

Scherzinger, W., Schumacher, H., 2004. Effects of forest management on forest-dwelling birds - a review. Vogelwelt 125, 215–250.

Sondenaa, A.C., 1991. The Wild Mammals of McDonald and Paul M. Dunn Forests, O.S.U. Research Forests, Corvallis, OR 39 pp.

Sota, T., 1996. Effect of capacity on resource input and the aquatic metazoan community structure in phytotelmata. Res Popul Ecol 38, 65-73.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment No. 42, Council of Europe Publishing, Strasbourg.

Speight, M.C.D., Castella, E., Sarthou, J.-P., Monteil, C., 2013. Species accounts of European Syrphidae (Diptera). Syrph the Net, the database of European Syrphidae. Syrph the Net Publications.

Stahl, P., Leger, F., 1992. Le Chat sauvage d'Europe. Encyclopédie des carnivores de France, vol 17. SFEPM.

Svensson, L., Mullarney, K., Zetterström, D., Grant, P.J., 2000. Le guide ornitho. Delachaux et Niestlé.

Stevenson, S.K., Rochelle, J.A., 1984. Lichen litterfall – its availability and utilization by black-tailed deer. In: Proceedings: Symposium on Fish and Wildlife Relationships in Old-Growth Forests, WR Meehan et al., eds., 391-396.

Thomas, A., Rosentreter, R., 1992. Utilization of lichens by pronghorn antelope in three valleys in east-central Idaho. Idaho Bureau of Land Management Technical Bulletin 92 (3), 13 pp.

Tillon, L., 2005. Biodiversité, dynamique et conservation des petits mammifères cavicoles en France. In: Vallauri, D. et al. (eds). Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, 137-142.

Ure, D.C., Maser, C., 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60, 3307-3315.

Vacher, J.P., Geniez, M., (ed.) 2010. Les Reptiles de France, Belgique, Luxembourg et Suisse. Collection Parthénope, Editions Biotope/Publications scientifiques du Muséum.

Vonhof, M.J., Gwilliam, J.C., 2007. Intra- and interspecific patterns of day roostselection by three species of forest-dwelling bats in Southern British Columbia. For. Ecol. Manage. 252, 165–175.

Wesołowski, T., 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. J Ornithol 148(S2), 395-405.

Bryophytes

Fritz, O., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (Fagus sylvatica). Biol Conserv 143, 1008-1016.

Meinunger, L., Schröder W., 2007. Verbreitungsatlas der Moose Deutschlands Band 1-3. Herausgegeben von Oliver Dürhammer für die Regensburgische Botanische Gesellschaft von 1790 e.V., Verlag der Gesellschaft, Regensburg.

Fungi

Aronsen, A., 1996. Mycena juniperina, a new member of section Supinae from Norway. Persoonia 16, 257-259.

Blackwell, M., 1984. Myxomycetes and their arthropods associates. In Wheeler Q. & Blackwell, M., (eds.). Fungus-Insect Relationships: perpestives in Ecology and Evolution. New York, Columbia University press, 67-90.

Corriol, G., 2005. Un Gymnopilus remarquable des vieilles sapinières pyrénéennes. Revista catalana de micologia 27, 49-54.

Darimont 1973 cited in Winterhoff W. (ed), 1992. Fungi in vegetation science. Kluwer Academic Publishers, Netherlands.

Ellis, M.B., Ellis, J.P., 1998. Microfungi on miscellaneous substrates. An identification handbook. Richmond Publishing, Slough, England.

Fritz, O., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (Fagus sylvatica). Biol Conserv 143, 1008-1016.

Gönczöl, J., Revay, A., 2003. Treehole fungal communities: aquatic, aeroaquatic and dematiaeous hyphomycetes. Fungal Diversity 12: 19-34.

Halama, M., Chachuła, P., Rutkowski, R., 2014. Mycena juniperina (agaricales, basidiomycota), new for the polish and central European mycobiota. Polish Botanical Journal 59 (1), 109-116.

Hertel, D., 2011. Tree roots in canopy soils of old European beech trees. An ecological reassessment of a forgotten phenomenon. Pedobiologia 54, 119-125.

Junninen K., Komonen A. 2011. Conservation ecology of boreal polypores: A review. Biological Conservation 144: 11–20.

Lisiewska, M., 1992. Macrofungi on special substrates. In: Winterhoff W (ed) Fungi in vegetation science. Kluwer, Netherlands, 151-182.

Moreno, G., Heykoop, M., Esteve-Raventos, F., Horak, E., 1997. Marasmiellus phaeomarasmioides spec nov (Tricholomataceae, Agaricales) from Spain. Persoonia 16, 405-411.

Niemelä, T., Wallenius, T., Kotiranta, H., 2002. The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Botanical Journal 47 (2), 91-101.

Ryvarden, L., Melo, I., 2014. Poroid fungi of Europe. Synopsis Fungorum 31, Fungiflora.Oslo, Norway.

Schigel, D.S., 2007. Fleshy fungi of the Genera Armillaria, Pleurotus and Grifola as habitatsx of Coleoptera. Karstenia 47, 37-48.

Seifert,K., Hughes,S., Boulay,H., Louis-Seize,G., 2007. Taxonomy, nomenclature and phylogeny of three cladosporium-like hyphomycetes, Sorocybe resinae, Seifertia azaleae and the Hormoconis anamorph of Amorphotheca resinae. Studies in Mycology, 235-245.

Villarreal, M., Esteve-Raventos, F., 1999. Mycena conicoalba, a new corticolous species from Spain. Österr.Z. Pilzk. 8, 15-34.

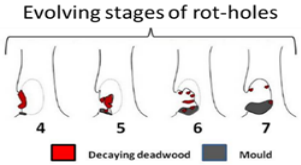
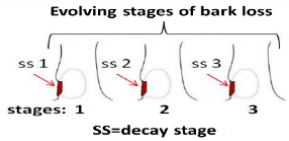
Wikars, L.-O., 2001. The wood-decaying fungus Daldinia loculata (Xylariaceae) as an indicator of fire-dependent insects. Ecological Bulletins 49, 263-268.

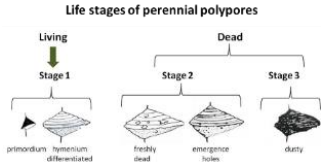
Lichens

Fritz, O., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (Fagus sylvatica). Biol Conserv 143, 1008-1016.

Spribille, T., Thor, G., Bunnell, F.L., Goward, T., Björk, C.R., 2008. Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. Ecography 31, 741-750.

Annexe 2 : Additional thresholds and features for intensive surveys (additional biodiversity studies and assessments). Tree base: height from ground <1m; tree trunk: height from the ground >1m. Ø: diameter.

TreM type	Additional thresholds	Location	Decay stage	Other characteristics
Small woodpecker breeding cavity			fresh (<5 y) vs old	Close to a polypore conk; associated with an epiphyte;
Medium-sized woodpecker breeding cavity		Branch vs trunk, dead vs "healthy" wood	fresh (<5 y) vs old	Close to a polypore conk; associated with an epiphyte; presence of a social insect nest (wasps, bees, ants)
Large woodpecker breeding cavity		Absolute height (m above ground)	fresh (<5 y) vs old	Close to a polypore conk; associated with an epiphyte; presence of a social insect nest (wasps, bees, ants)
Woodpecker "flute" (breeding cavity string)			fresh (<5 y) vs old	Medium-sized vs large woodpecker cavities; close to a polypore conk; associated with an epiphyte; number of entrances; closed vs open top; presence of a social insect nest (wasps, bees, ants)
Trunk base rot-hole Trunk rot-hole Semi-open trunk rot-hole Chimney trunk base rot-hole Chimney trunk rot-hole	Entrance ø: 3-10cm, >20cm	Trunk base vs branch-free-trunk vs trunk part within canopy	Development stage (4-7) 	Chamber volume (only for base cavities): small: <20 dm³, medium 20-100 dm³, large >100 dm³; presence of a social insect nest (wasps, bees, ants)
Hollow branch				Entrance diameter (3-10, 11-20, >20 cm)
Insect galleries and bore holes				
Dendrotelm (phytotelmata, water-filled hole)	Largest ø : 3-15cm, >30 cm	Base vs other position (trunk, crown)		Bark-lined vs rotted bottom
Woodpecker foraging excavation		Base vs trunk		
Trunk bark-lined concavity		Base vs trunk		
Root buttress concavity	Entrance ø: 3-10cm, >20cm			
Bark loss	Surface of exposed wood: 100-300cm² (<A5 format), 600 (A4 format)-10,000 cm², >1m²		Development stage (1-3) 	
Fire scar	Surface >1m²			
Bark shelter				Presence of a bird nest
Bark pocket				Presence of organic material or mould
Stem breakage	ø of the broken part			Simple vs splintered
Limb breakage (heartwood exposed)	Surface of exposed wood: Area 300-600 cm² (A5-A4 format), 600 (A4 format)-10,000 cm², >1m²			Simple vs splintered

TreM type	Additional thresholds	Location	Decay stage	Other characteristics
Crack	Length: 1-2m, >2m	Base vs trunk		Wet vs dry
Lightning scar				
Fork split at the insertion				
Dead branches	Number or semi-quantitative % of dead crown volume: 10-25%, 26-50%, 51-75%, > 75%			Sun-exposed vs shady
Dead top	ø at the base of the dead part			
Remaining broken limb	ø of the broken branch		Decay stage (1-4)	Simple vs splintered
Witch broom				
Epicormic shoots				
Burr				
Decayed canker				
Perennial polypore	Number of conks		Life stage (1-3) 	Fungi genus
Annual polypore				Fungi genus
Pulpy agaric				Fungi genus
Large pyrenomycete				Fungi genus
Myxomycetes				"Fungi" genus
Bryophytes	% of the trunk area covered: 10-25%, 26-50%, 51-75%, >75%	Trunk vs crown		
Foliose and fruticose lichens		Trunk vs crown		
Ivy and lianas		Trunk vs crown		
Ferns	1-5 fronds, >5 fronds			Fern species
Mistletoe	Number of mistletoe clusters or % of the crown infected: <25%, >25%			
Vertebrate nest	ø: 26-80cm, > 80cm			Occupation, species
Invertebrate nest				Invertebrate taxon
Bark microsoil				
Crown microsoil				
Sap run	Cumulative length: 21-50cm, >50cm			
Heavy resinosis	Cumulative length: 21-50cm, >50cm			

Annexes B : Nothing else matters? A nationwide study of microhabitats drivers at the tree scale – Supplementary materials

Yoan Paillet*, Nicolas Debaive, Frédéric Archaux, Vincent Boulanger, Olivier Gilg, Eric Guilbert

Manuscript preprint

*Annexe 3 : Model scaled estimations for number of microhabitat types per tree issued from a generalised linear mixed model with Poisson error distribution and plot nested in site as a random effect. DBH: Diameter at Breast Height; PC1 and PC2: eigenvalues for the first two axes of a principal component analysis on biogeoclimatic variables (see main text); SE: standard error of the mean: p = p value; ***p<0.001; **p<0.01; *p<0.05.*

Parameter	Estimate	SE	p	
Intercept(Beech)	0.804	0.096	<0.001	***
DBH	0.209	0.036	<0.001	***
Fir	-0.302	0.046	<0.001	***
Oak	0.220	0.050	<0.001	***
Pine	-0.316	0.078	0.0001	***
Spruce	-0.406	0.053	<0.001	***
Living trees	-0.270	0.032	<0.001	***
PC1	-0.064	0.018	<0.001	***
PC2	0.033	0.025	0.1963	ns
DBH:Fir	-0.040	0.047	0.3986	ns
DBH:Oak	0.002	0.048	0.9728	ns
DBH:Pine	-0.090	0.089	0.3158	ns
DBH:Spruce	-0.028	0.054	0.6094	ns
DBH:Living	-0.008	0.0370	0.8284	ns
Fir:Living	0.006	0.0480	0.8984	ns
Oak:Living	-0.157	0.049	0.0014	**
Pine:Living	-0.089	0.079	0.2605	ns
Spruce:Living	0.029	0.055	0.5959	ns
DBH:Fir:Living	-0.098	0.049	0.0478	*
DBH:Oak:Living	-0.014	0.049	0.7714	ns
DBH:Pine:Living	0.195	0.097	0.0458	*
DBH:Spruce:Living	-0.118	0.057	0.0389	*

Annexe 4 : Accumulation levels of microhabitat per tree (number of microhabitats and occurrence) for a Diameter at Breast Height (DBH) increment from 50cm to 100cm.

	Living trees					Dead trees				
Microhabitats	Beech	Fir	Oak	Pine	Spruce	Beech	Fir	Oak	Pine	Spruce
All	1.185	0.235	1.027	1.487	0.191	1.653	0.960	1.824	0.614	0.979
Base cavities	0.154	0.065	0.036	0.099	0.1	0.335	0.077	0.041	-0.005	0.222
Trunk cavities	0.056	0.013	0.033	0.05	0.017	0.323	0.068	0.262	0.013	0.048
Canopy cavities	0.017	0.001	0.016	0.004	0	0	0.065	0.014	0	0.009
Woodp. cavities	0.01	0.002	0.012	0.083	0.017	0.041	0.032	0.009	0.075	0.026
Cracks	0.032	0.001	0.018	0.02	0.009	0.078	-0.004	0.012	-0.002	-0.003
Woodp. feeding holes	0.029	0.003	0.036	0.027	0.005	0.441	0.285	0.392	0.063	0.223
Rot	0.018	0.012	0.005	0.016	0	0.255	0.009	0.239	0.082	-0.02
Injuries	0.048	-0.009	0.049	0.021	-0.021	-0.005	-0.003	0.006	0.012	-0.004
Conks of fungi	0.04	0.006	0.011	0.005	-0.001	0.154	0.245	0.136	-0.01	0.277
Bark characteristics	0.007	0.001	0.003	0.002	0	0.045	0.087	0.155	0.04	-0.036
Moss cover >50%	0.178	0.228	-0.011	-0.017	0.112	0.087	0.179	0.009	0.722	0.315
Lichen cover > 50%	0.067	0.126	0.021	0.068	-0.031	-0.013	0.006	0.007	-0.036	0.009
Ivy cover >50%	0.001	0.002	0.02	0	0.003	0.001	0	0	0.013	0
Small branches	0.138	0.363	0.209	0.283	0.465	-0.005	0.055	-0.015	-0.023	0.011
Medium branches	0.32	0.117	0.528	0.688	0.064	0.018	0.024	0.01	-0.019	0.016
Large branches	0.049	0.001	0.078	0.145	0.004	0.023	0.006	0.001	0.244	0
Crown skeleton	0	0.002	0	0.026	0.003	0	0	0.001	0.065	-0.004
Forks	0.244	0.005	0.07	0.159	0.002	-0.002	0.018	0.001	-0.001	0.038
Broken stem	0.016	-0.024	-0.005	-0.028	-0.015	0.12	0.021	0.063	-0.021	0.045

*Annexe 5 : Model scaled estimations for occurrence of microhabitat types per tree issued from a generalised linear mixed model with binomial error distribution and plot nested in site as a random effect. DBH: Diameter at Breast Height; PC1 and PC2: eigenvalues for the first two axes of a principal component analysis on biogeoclimatic variables (see main text); SE: standard error of the mean: p = p value; ***p<0.001; **p<0.01; *p<0.05.*

	Base cavities				Trunk cavities				Canopy cavities				Woodpecker cavities				Cracks				Woodpecker feeding holes			
	Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p	
Intercept	-2.66	0.34	0.00	***	-2.50	0.26	0.00	***	-6.76	1.02	0.00	***	-3.48	0.32	0.00	***	-3.54	0.32	0.00	***	-0.95	0.29	0.00	**
DBH	0.85	0.21	0.00	***	0.77	0.19	0.00	***	-0.12	1.18	0.92	ns	0.36	0.25	0.16	ns	0.52	0.22	0.02	*	0.77	0.19	0.00	***
Fir	-1.11	0.33	0.00	**	-1.19	0.28	0.00	***	-1.34	1.94	0.49	ns	-1.67	0.52	0.00	**	-1.09	0.35	0.00	**	0.43	0.23	0.07	.
Oak	-1.10	0.35	0.00	**	-0.54	0.32	0.09	.	0.76	1.07	0.48	ns	-0.48	0.45	0.28	ns	0.44	0.36	0.22	ns	0.35	0.27	0.19	ns
Pine	-2.09	0.59	0.00	***	-1.29	0.50	0.01	*	-10.38	14.62	0.48	ns	-0.54	0.59	0.36	ns	-2.51	0.72	0.00	***	-0.94	0.36	0.01	*
Spruce	-1.50	0.32	0.00	***	-2.07	0.41	0.00	***	-2.05	2.06	0.32	ns	-2.12	0.60	0.00	***	-0.56	0.37	0.13	ns	-0.58	0.26	0.03	*
Living	-0.48	0.19	0.01	*	-1.04	0.17	0.00	***	0.42	0.97	0.66	ns	-2.10	0.28	0.00	***	-0.62	0.19	0.00	**	-4.72	0.23	0.00	***
PC1	-0.34	0.11	0.00	**	-0.28	0.09	0.00	**	0.14	0.17	0.43	ns	0.01	0.10	0.95	ns	-0.09	0.10	0.39	ns	0.25	0.10	0.01	*
PC2	-0.10	0.17	0.55	ns	0.02	0.15	0.87	ns	0.00	0.26	0.99	ns	-0.22	0.16	0.17	ns	0.04	0.17	0.83	ns	-0.12	0.17	0.46	ns
DBH:Fir	-0.32	0.32	0.31	ns	-0.30	0.28	0.28	ns	2.09	1.41	0.14	ns	0.35	0.43	0.42	ns	-0.70	0.39	0.07	.	-0.30	0.23	0.19	ns
DBH:Oak	-0.30	0.30	0.32	ns	0.19	0.26	0.48	ns	0.74	1.23	0.55	ns	-0.21	0.39	0.60	ns	-0.40	0.32	0.21	ns	0.23	0.27	0.41	ns
DBH:Pine	-1.07	0.63	0.09	.	-0.62	0.53	0.24	ns	-9.16	11.85	0.44	ns	0.23	0.59	0.69	ns	-1.41	0.73	0.06	.	-0.56	0.35	0.11	ns
DBH:Spruce	0.10	0.32	0.75	ns	-0.22	0.35	0.54	ns	1.67	1.40	0.23	ns	0.41	0.42	0.33	ns	-0.59	0.36	0.10	.	-0.28	0.26	0.27	ns
DBH:Living	-0.19	0.21	0.36	ns	-0.34	0.19	0.08	.	0.98	1.19	0.41	ns	0.14	0.27	0.59	ns	-0.09	0.23	0.70	ns	0.06	0.21	0.76	ns
Fir:Living	-0.13	0.35	0.70	ns	-0.90	0.34	0.01	**	-0.48	2.14	0.82	ns	1.20	0.57	0.04	*	-0.26	0.39	0.50	ns	-0.56	0.35	0.11	ns
Oak:Living	0.42	0.35	0.23	ns	-0.09	0.31	0.79	ns	-0.80	1.07	0.46	ns	0.55	0.47	0.24	ns	-1.80	0.38	0.00	***	0.47	0.30	0.11	ns
Pine:Living	-0.71	0.58	0.22	ns	-0.92	0.53	0.09	.	9.82	14.63	0.50	ns	0.51	0.59	0.39	ns	1.46	0.65	0.02	*	1.11	0.42	0.01	**
Spruce:Living	1.24	0.32	0.00	***	-1.58	0.61	0.01	*	-10.06	105.3	0.92	ns	1.52	0.63	0.02	*	-0.67	0.42	0.11	ns	0.10	0.36	0.78	ns
DBH:Fir:Living	0.27	0.33	0.41	ns	0.37	0.32	0.24	ns	-2.48	1.55	0.11	ns	-0.65	0.48	0.17	ns	0.38	0.42	0.36	ns	-0.25	0.31	0.42	ns
DBH:Oak:Living	0.17	0.31	0.59	ns	-0.06	0.27	0.82	ns	-0.82	1.24	0.51	ns	0.20	0.40	0.62	ns	0.66	0.33	0.05	.	-0.54	0.29	0.06	.
DBH:Pine:Living	1.64	0.70	0.02	*	1.14	0.64	0.07	.	8.95	11.87	0.45	ns	0.39	0.67	0.57	ns	1.53	0.75	0.04	*	0.53	0.48	0.27	ns
DBH:Spruce:Living	-0.29	0.33	0.38	ns	0.81	0.44	0.07	.	-1.73	69.75	0.98	ns	-0.10	0.46	0.83	ns	0.55	0.39	0.16	ns	-0.01	0.33	0.98	ns

Annexe 5 (continued)

	Rot				Injuries				Conks of fungi				Bark characteristics				Moss (>50%)				Lichen (>50%)			
	Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p	
Intercept	-3.39	0.34	0.00	***	-4.49	0.40	0.00	***	-0.37	0.22	0.09	.	-2.65	0.35	0.00	***	0.05	0.63	0.93	ns	-4.03	0.73	0.00	***
DBH	0.88	0.21	0.00	***	-0.36	0.36	0.32	ns	0.25	0.15	0.08	.	0.22	0.19	0.25	ns	0.14	0.19	0.46	ns	-0.37	0.27	0.17	ns
Fir	-0.80	0.31	0.01	*	-0.67	0.45	0.13	ns	-0.69	0.20	0.00	***	-0.19	0.30	0.54	ns	-1.75	0.25	0.00	***	0.63	0.29	0.03	*
Oak	1.54	0.32	0.00	***	-0.18	0.53	0.74	ns	-2.01	0.26	0.00	***	1.81	0.29	0.00	***	-1.10	0.28	0.00	***	1.37	0.42	0.00	**
Pine	-0.62	0.59	0.29	ns	-0.31	0.48	0.52	ns	-2.47	0.53	0.00	***	-0.15	0.46	0.75	ns	-2.30	0.52	0.00	***	1.25	0.44	0.01	**
Spruce	-0.19	0.32	0.55	ns	-0.64	0.59	0.28	ns	-1.45	0.26	0.00	***	0.47	0.30	0.12	ns	-2.45	0.29	0.00	***	-0.62	0.30	0.04	*
Living	-0.85	0.22	0.00	***	1.87	0.30	0.00	***	-4.47	0.17	0.00	***	-2.98	0.21	0.00	***	0.82	0.16	0.00	***	1.88	0.21	0.00	***
PC1	-0.23	0.11	0.03	*	0.06	0.07	0.41	ns	0.32	0.09	0.00	**	0.10	0.14	0.49	ns	0.16	0.15	0.28	ns	-0.76	0.18	0.00	***
PC2	0.18	0.17	0.31	ns	-0.30	0.12	0.01	*	0.53	0.15	0.00	***	-0.10	0.22	0.64	ns	-0.21	0.20	0.30	ns	0.80	0.25	0.00	**
DBH:Fir	-0.72	0.28	0.01	*	-0.35	0.54	0.52	ns	0.17	0.19	0.36	ns	0.18	0.26	0.48	ns	0.27	0.27	0.33	ns	0.41	0.34	0.23	ns
DBH:Oak	-0.29	0.27	0.28	ns	0.52	0.51	0.30	ns	0.09	0.22	0.69	ns	0.03	0.27	0.90	ns	-0.12	0.28	0.65	ns	0.52	0.46	0.26	ns
DBH:Pine	-0.25	0.55	0.65	ns	0.66	0.55	0.23	ns	-0.44	0.61	0.47	ns	0.00	0.47	1.00	ns	1.32	0.66	0.05	*	0.03	0.52	0.95	ns
DBH:Spruce	-1.26	0.33	0.00	***	-0.42	0.73	0.56	ns	0.37	0.25	0.13	ns	-0.46	0.29	0.11	ns	0.65	0.31	0.03	*	0.50	0.37	0.19	ns
DBH:Living	-0.58	0.21	0.01	**	0.59	0.36	0.10	.	0.37	0.16	0.02	*	0.17	0.21	0.40	ns	0.38	0.19	0.05	.	0.58	0.28	0.04	*
Fir:Living	0.33	0.33	0.32	ns	0.65	0.45	0.15	ns	-0.49	0.35	0.16	ns	-1.00	0.39	0.01	*	0.25	0.25	0.33	ns	0.08	0.29	0.79	ns
Oak:Living	-2.23	0.33	0.00	***	-0.27	0.53	0.61	ns	1.75	0.27	0.00	***	-2.21	0.31	0.00	***	1.87	0.28	0.00	***	-1.19	0.41	0.00	**
Pine:Living	-1.88	0.66	0.01	**	-0.47	0.46	0.31	ns	0.97	0.89	0.28	ns	-1.32	0.68	0.05	.	-2.15	0.55	0.00	***	-1.37	0.47	0.00	**
Spruce:Living	-1.43	0.39	0.00	***	0.88	0.59	0.14	ns	0.33	0.45	0.46	ns	-2.06	0.48	0.00	***	-0.98	0.30	0.00	**	0.16	0.30	0.61	ns
DBH:Fir:Living	0.71	0.30	0.02	*	0.05	0.55	0.93	ns	-0.23	0.27	0.40	ns	-0.26	0.33	0.43	ns	-0.41	0.28	0.15	ns	-0.40	0.35	0.26	ns
DBH:Oak:Living	0.26	0.28	0.36	ns	-0.49	0.51	0.34	ns	-0.42	0.24	0.08	.	-0.19	0.28	0.51	ns	-0.43	0.28	0.12	ns	-0.51	0.47	0.27	ns
DBH:Pine:Living	0.90	0.72	0.22	ns	-0.72	0.57	0.20	ns	0.47	1.22	0.70	ns	0.03	0.96	0.98	ns	-2.39	0.72	0.00	**	-0.02	0.57	0.97	ns
DBH:Spruce:Living	0.98	0.37	0.01	**	0.04	0.74	0.96	ns	-1.42	0.45	0.00	**	-0.12	0.44	0.79	ns	-0.72	0.33	0.03	*	-0.79	0.39	0.04	*

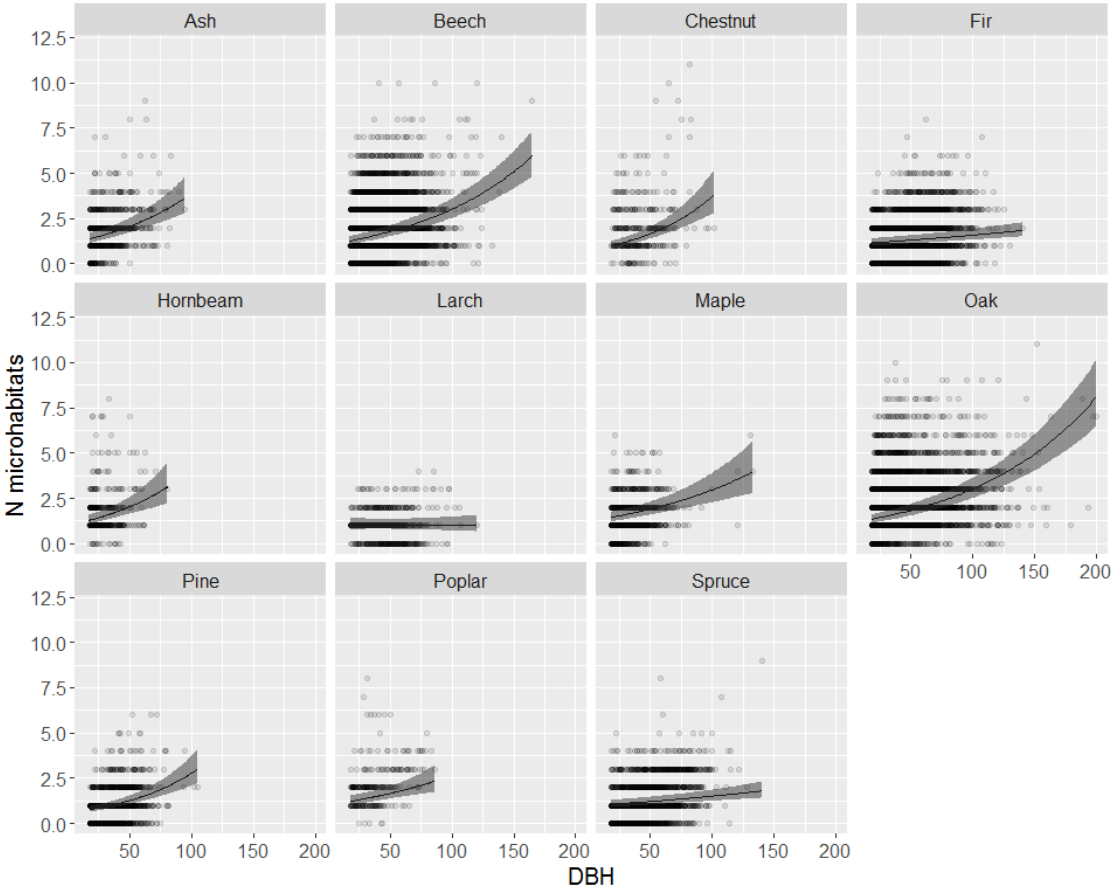
Annexe 5 (continued)

	Ivy (>50%)				Small branches				Medium branches				Large branches				Crown skeleton				Forks			
	Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p		Estimate	SE	p	
Intercept	-6.61	0.62	0.00	***	-4.36	0.43	0.00	***	-4.49	0.35	0.00	***	-5.95	0.60	0.00	***	-5.76	1.02	0.00	***	-6.14	0.80	0.00	***
DBH	0.22	0.39	0.57	ns	-0.19	0.35	0.58	ns	0.37	0.34	0.28	ns	0.79	0.50	0.11	ns	-0.01	0.30	0.99	ns	-1.40	0.77	0.07	.
Fir	-0.65	0.56	0.24	ns	1.00	0.35	0.01	**	1.60	0.33	0.00	***	-1.83	1.49	0.22	ns	-1.98	0.70	0.01	**	0.36	0.77	0.64	ns
Oak	1.14	0.46	0.01	*	0.38	0.43	0.38	ns	1.35	0.36	0.00	***	-0.23	0.84	0.79	ns	-0.12	0.40	0.77	ns	2.24	0.85	0.01	**
Pine	0.32	0.91	0.72	ns	1.19	0.48	0.01	*	1.51	0.50	0.00	**	1.33	0.82	0.11	ns	-0.02	0.52	0.96	ns	0.38	1.03	0.72	ns
Spruce	0.42	0.51	0.42	ns	0.65	0.45	0.14	ns	-1.69	1.32	0.20	ns	-39.07	49109.68	1.00	ns	1.32	0.46	0.00	**	0.22	0.80	0.78	ns
Living	0.20	0.39	0.61	ns	2.52	0.29	0.00	***	1.39	0.27	0.00	***	-0.65	0.55	0.24	ns	-4.95	0.50	0.00	***	3.73	0.73	0.00	***
PC1	0.87	0.19	0.00	***	0.10	0.08	0.18	ns	0.07	0.08	0.41	ns	0.14	0.14	0.31	ns	0.44	0.16	0.01	**	-0.56	0.10	0.00	***
PC2	-0.95	0.28	0.00	**	0.02	0.13	0.91	ns	-0.07	0.13	0.59	ns	0.35	0.22	0.11	ns	-0.19	0.32	0.55	ns	0.62	0.13	0.00	***
DBH:Fir	0.02	0.47	0.96	ns	0.60	0.40	0.13	ns	-0.21	0.40	0.60	ns	0.23	0.95	0.81	ns	-0.03	0.80	0.97	ns	1.96	0.81	0.02	*
DBH:Oak	-0.21	0.44	0.63	ns	-0.84	0.51	0.10	.	-0.29	0.41	0.49	ns	-0.71	0.74	0.34	ns	0.07	0.35	0.84	ns	1.43	0.87	0.10	ns
DBH:Pine	0.61	1.19	0.61	ns	-1.13	0.54	0.04	*	-0.60	0.58	0.30	ns	0.62	0.84	0.46	ns	1.25	0.45	0.01	**	1.30	1.10	0.24	ns
DBH:Spruce	-0.38	0.52	0.47	ns	0.36	0.45	0.42	ns	0.45	0.79	0.57	ns	-21.37	39120.97	1.00	ns	-0.71	0.49	0.15	ns	2.14	0.81	0.01	**
DBH:Living	0.04	0.39	0.93	ns	0.53	0.35	0.13	ns	0.56	0.34	0.10	ns	0.48	0.51	0.34	ns	0.09	0.43	0.84	ns	2.00	0.77	0.01	*
Fir:Living	0.73	0.54	0.18	ns	-1.30	0.35	0.00	***	-3.86	0.38	0.00	***	-0.18	1.72	0.92	ns	3.44	0.83	0.00	***	-1.90	0.77	0.01	*
Oak:Living	-0.23	0.46	0.61	ns	0.63	0.43	0.15	ns	0.13	0.36	0.71	ns	1.81	0.86	0.03	*	0.53	0.57	0.36	ns	-2.57	0.85	0.00	**
Pine:Living	-0.56	0.96	0.56	ns	0.36	0.47	0.45	ns	-0.46	0.49	0.35	ns	-0.53	0.89	0.55	ns	2.92	0.58	0.00	***	-1.51	1.04	0.15	ns
Spruce:Living	0.21	0.52	0.69	ns	-1.55	0.46	0.00	**	-0.39	1.36	0.78	ns	33.54	49109.68	1.00	ns	1.95	0.65	0.00	**	-2.08	0.80	0.01	**
DBH:Fir:Living	0.19	0.48	0.70	ns	-0.15	0.40	0.71	ns	0.51	0.42	0.22	ns	-0.73	1.06	0.49	ns	1.14	0.89	0.20	ns	-2.50	0.81	0.00	**
DBH:Oak:Living	0.21	0.44	0.63	ns	0.85	0.51	0.09	.	0.30	0.41	0.47	ns	0.33	0.74	0.66	ns	0.58	0.48	0.23	ns	-1.46	0.87	0.10	.
DBH:Pine:Living	-1.04	1.28	0.42	ns	1.27	0.55	0.02	*	1.03	0.60	0.09	.	-0.32	0.93	0.73	ns	0.27	0.57	0.63	ns	-1.18	1.11	0.29	ns
DBH:Spruce:Living	0.63	0.54	0.24	ns	0.38	0.46	0.41	ns	-0.42	0.82	0.61	ns	22.46	39120.97	1.00	ns	1.52	0.63	0.02	*	-2.71	0.82	0.00	**

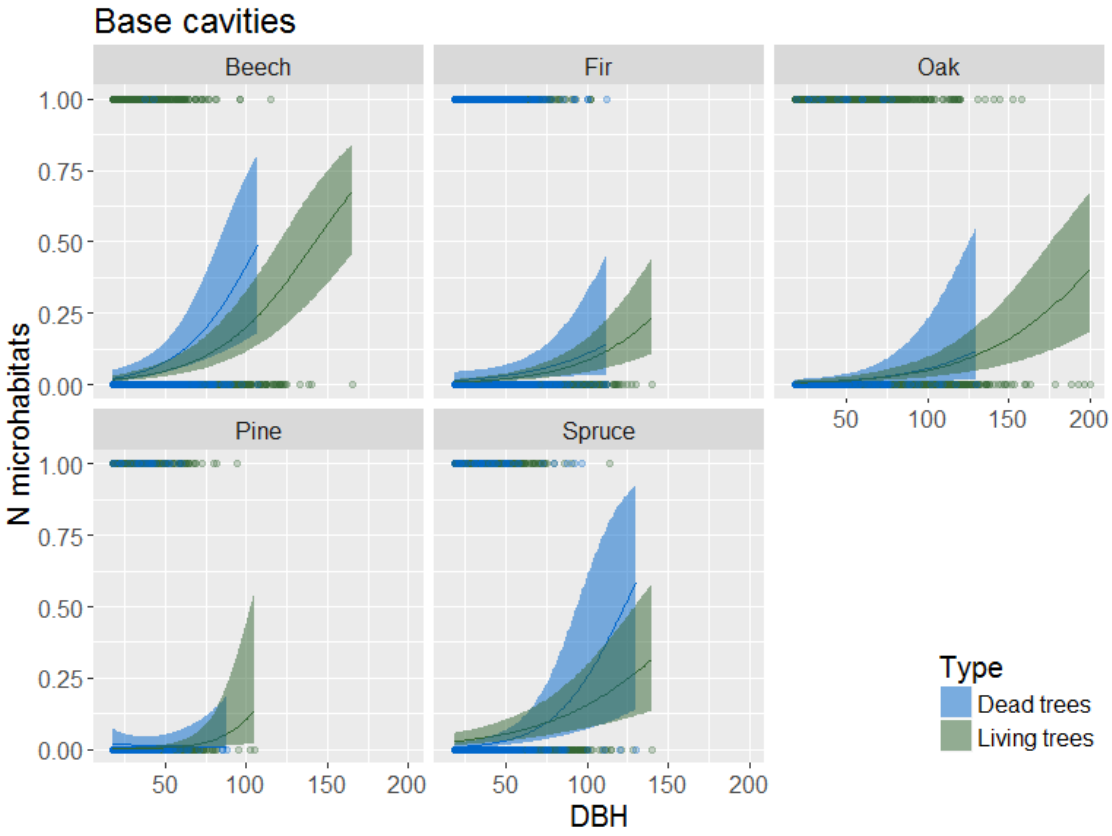
Annexe 5 (continued)

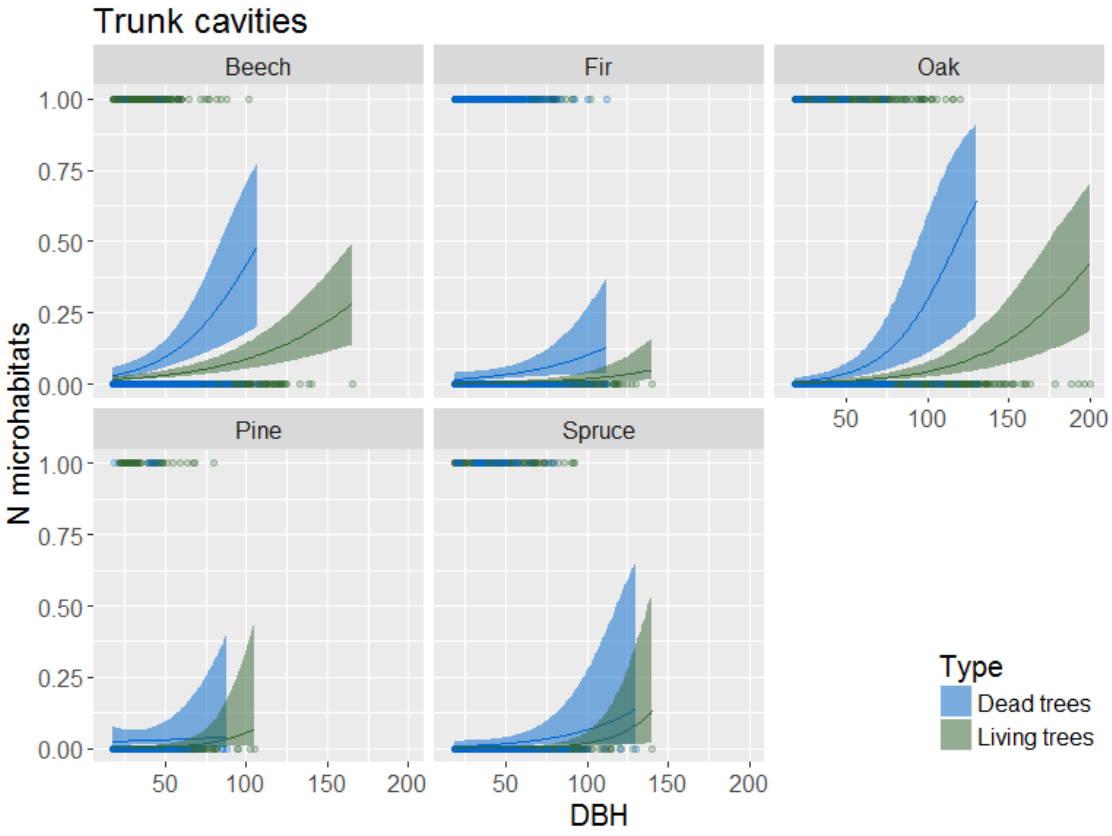
	Broken stems			
	Estimate	SE	p	
Intercept	-3.66	0.36	0.00	***
DBH	0.72	0.24	0.00	**
Fir	0.28	0.30	0.36	ns
Oak	-0.23	0.43	0.59	ns
Pine	-0.09	0.49	0.85	ns
Spruce	-0.08	0.34	0.81	ns
Living	-0.17	0.26	0.53	ns
PC1	-0.14	0.09	0.11	ns
PC2	-0.22	0.14	0.10	.
DBH:Fir	-0.53	0.29	0.07	.
DBH:Oak	-0.12	0.33	0.72	ns
DBH:Pine	-1.57	0.50	0.00	**
DBH:Spruce	-0.33	0.31	0.28	ns
DBH:Living	-0.49	0.24	0.04	*
Fir:Living	0.09	0.31	0.76	ns
Oak:Living	0.18	0.44	0.68	ns
Pine:Living	0.53	0.49	0.28	ns
Spruce:Living	0.20	0.36	0.57	ns
DBH:Fir:Living	-0.39	0.30	0.18	ns
DBH:Oak:Living	-0.26	0.34	0.45	ns
DBH:Pine:Living	0.70	0.53	0.19	ns
DBH:Spruce:Living	-0.31	0.33	0.35	ns

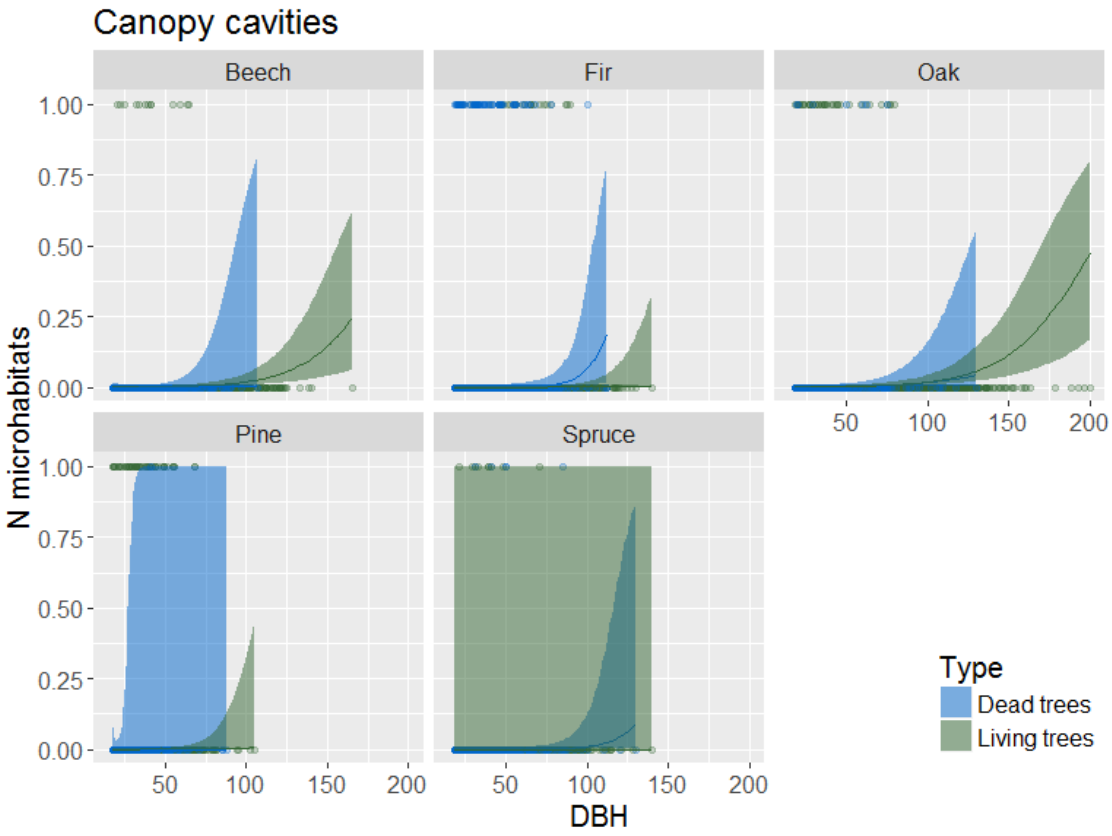
Annexe 6 : Relationship between total number of microhabitats per tree and Diameter at Breast Height (DBH) by species and live status (living vs dead standing trees). The line represents the estimation issued from a generalized mixed effect mode with Poisson error distribution. The ribbon represents the 95% confidence interval of the mean. Principal component analysis eigenvalues were hold constant for the representation.

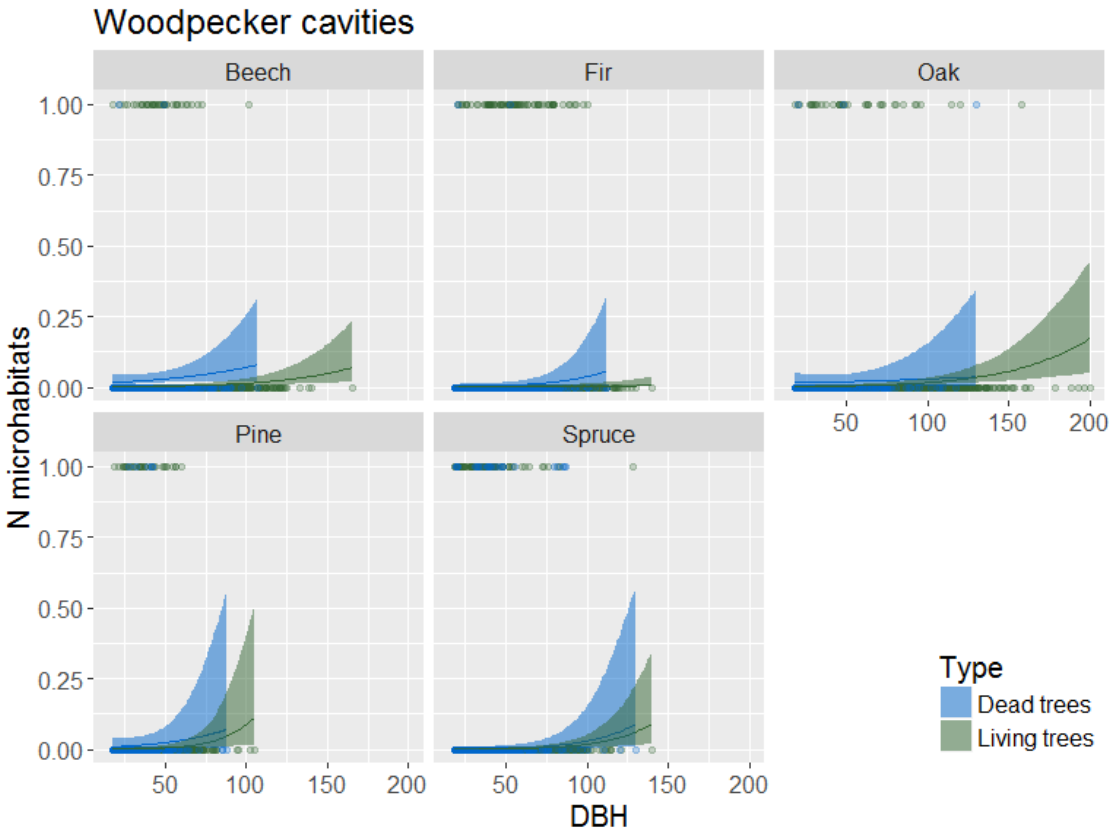


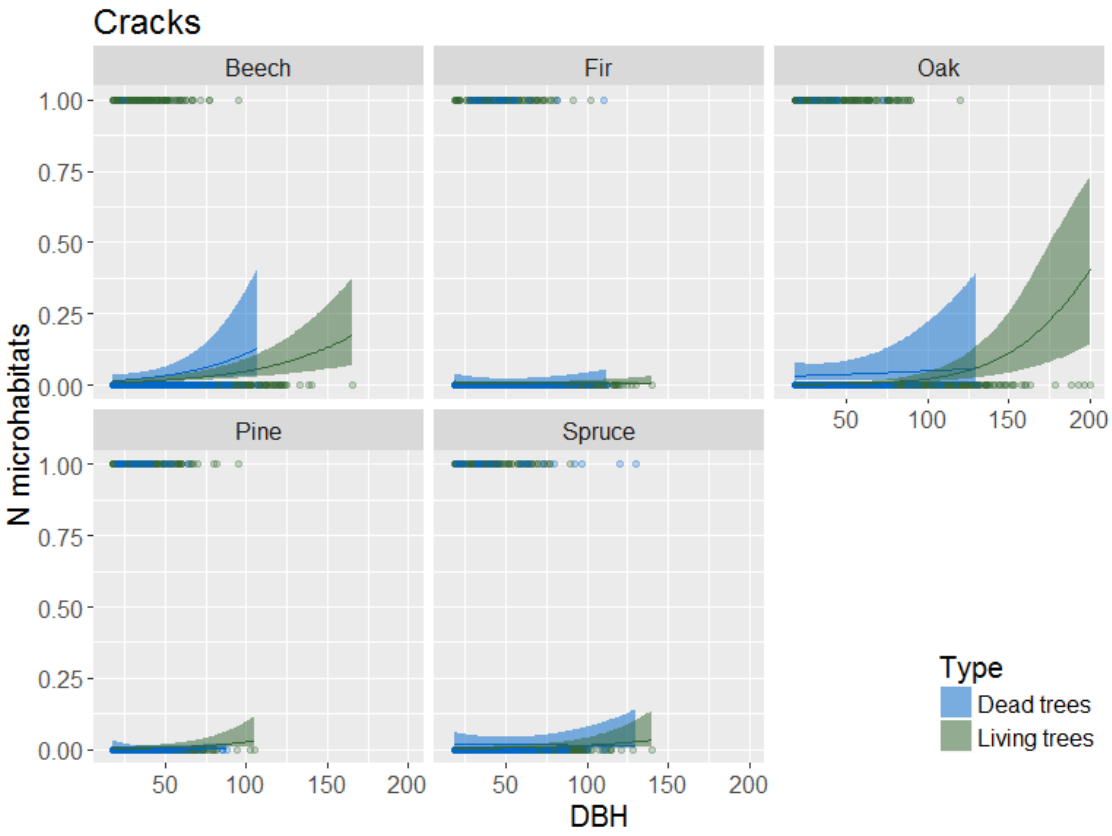
Annexe 7 : Relationship between occurrence of microhabitats per tree and Diameter at Breast Height (DBH) by species and live status (living vs dead standing trees). The line represents the estimation issued from a generalized mixed effect mode with Binomial error distribution. The ribbons represent the 95% confidence interval of the mean. Principal component analysis eigenvalues were hold constant for the representation.

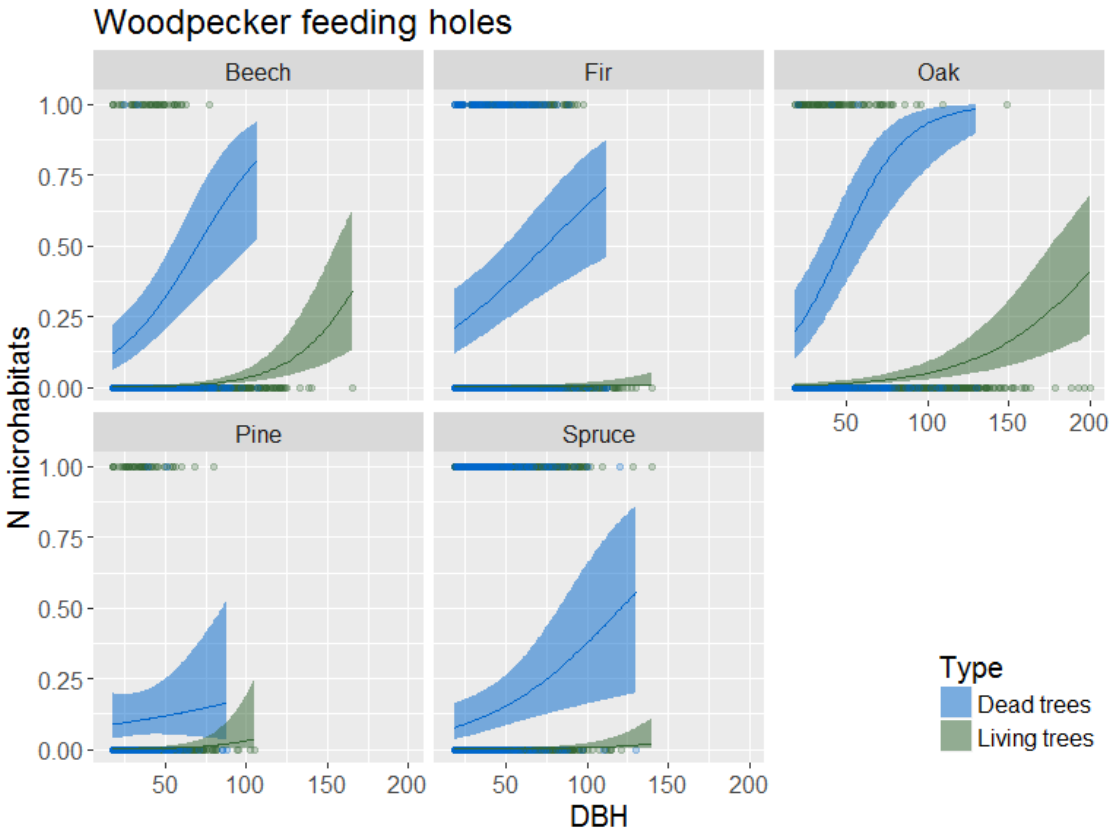


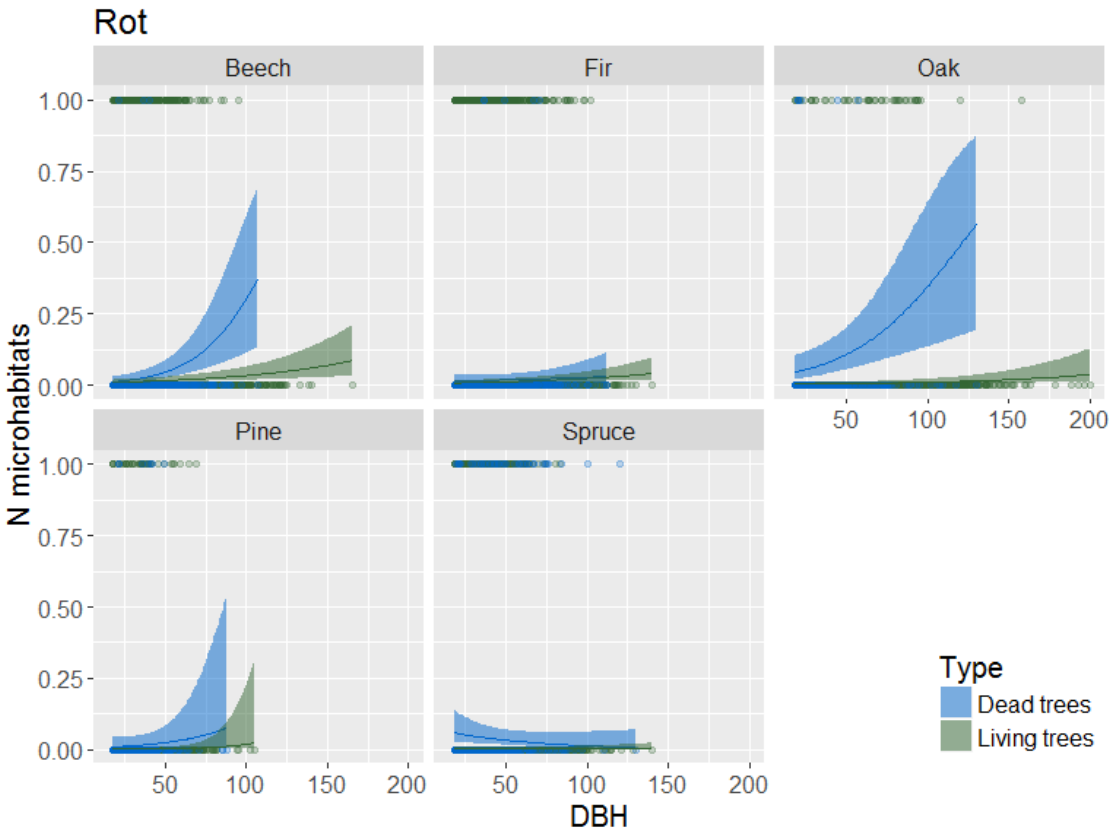


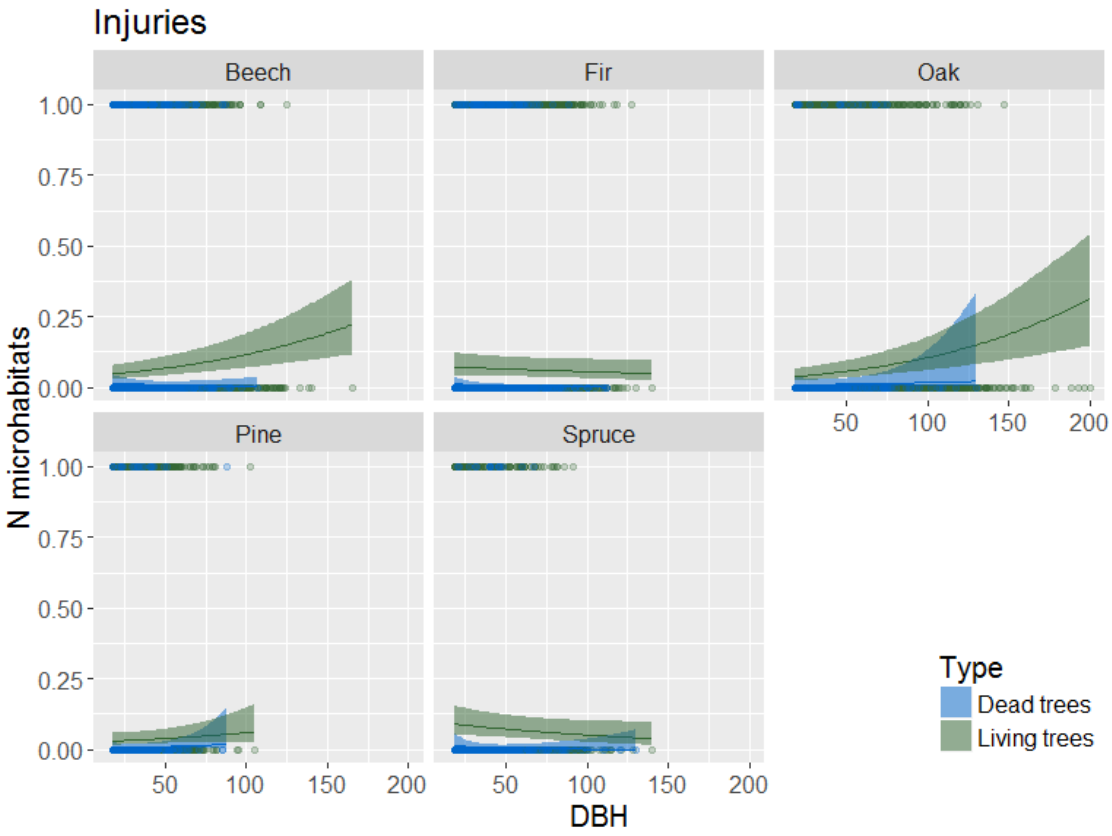

Canopy cavities
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

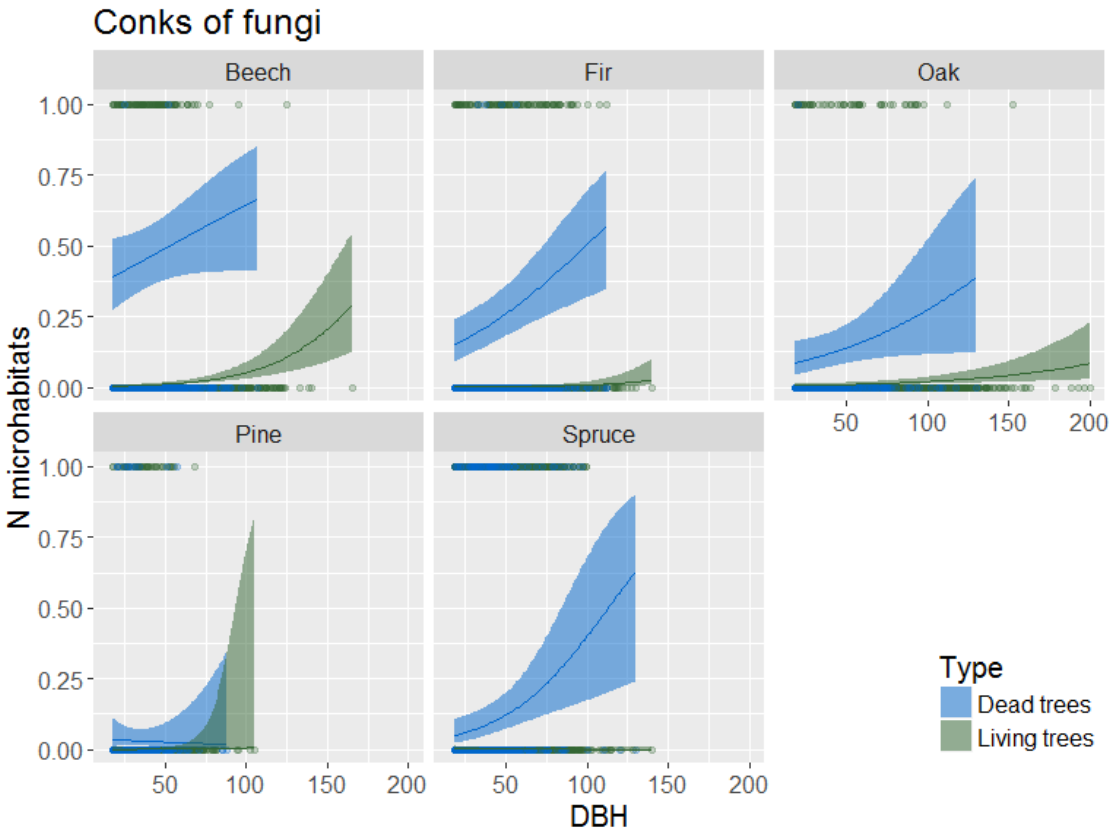

Woodpecker cavities
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Cracks
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

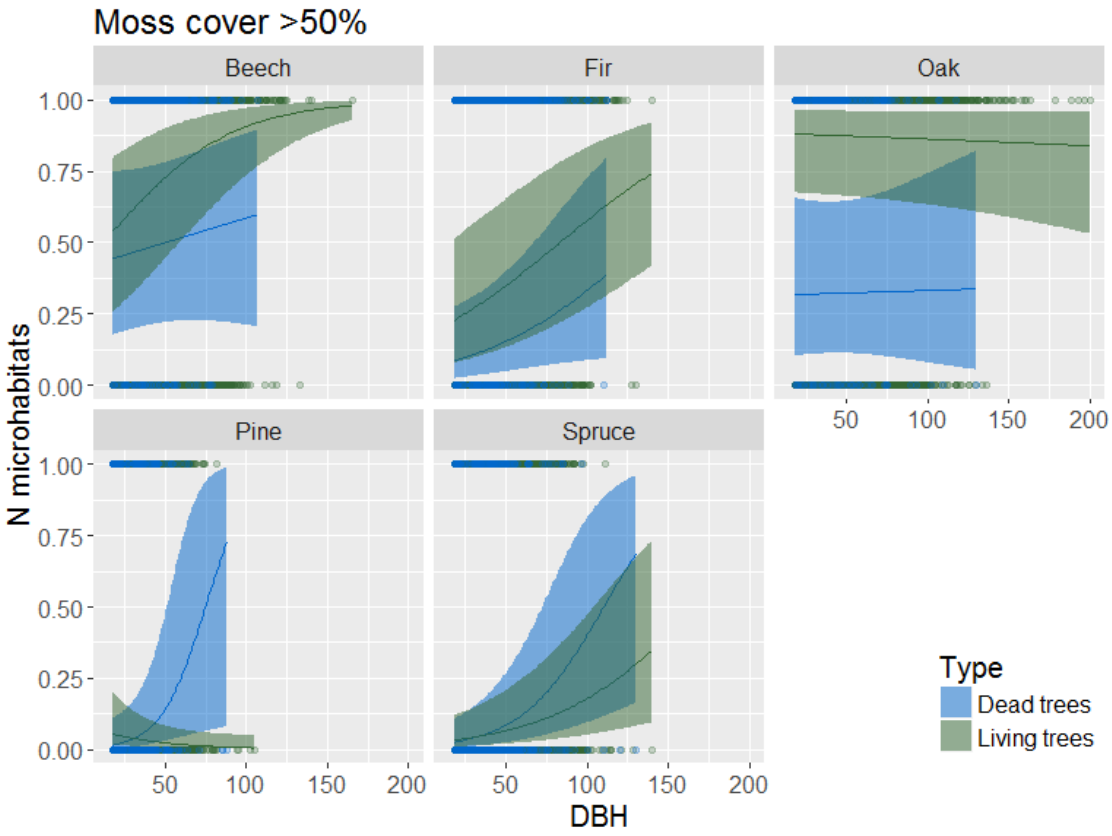

Woodpecker feeding holes
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

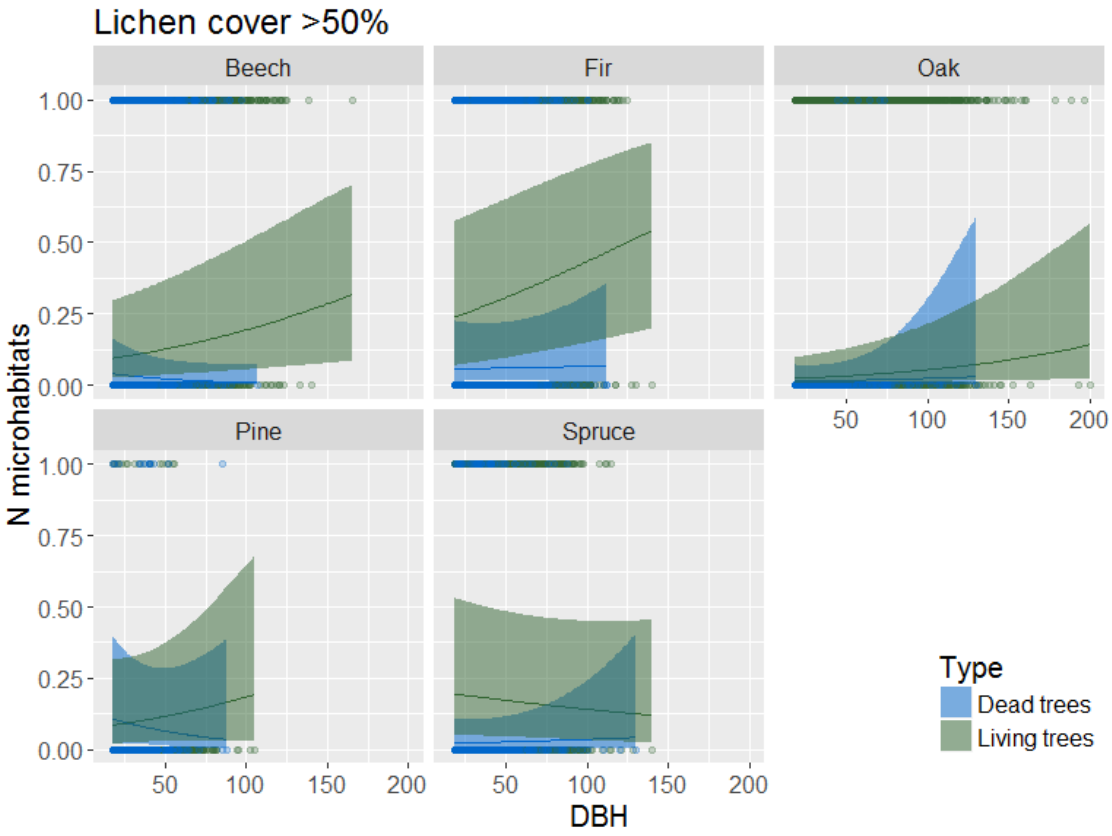

Rot
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

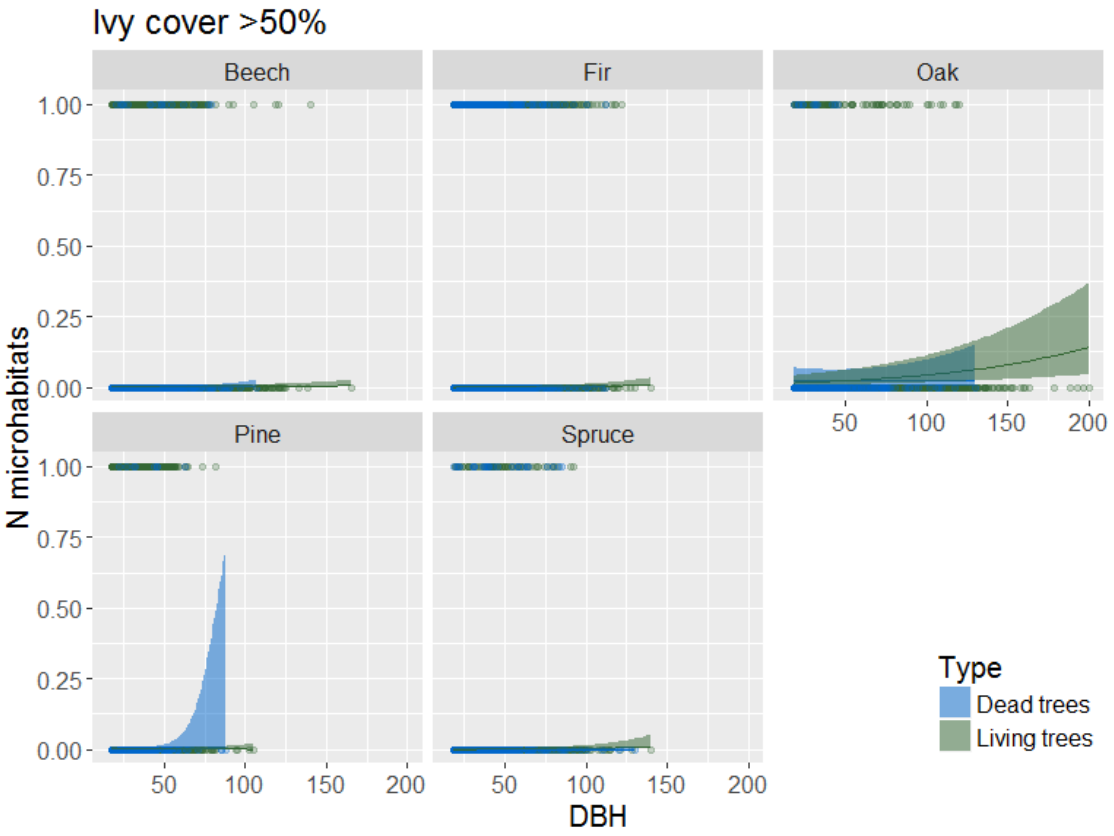

Injuries
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

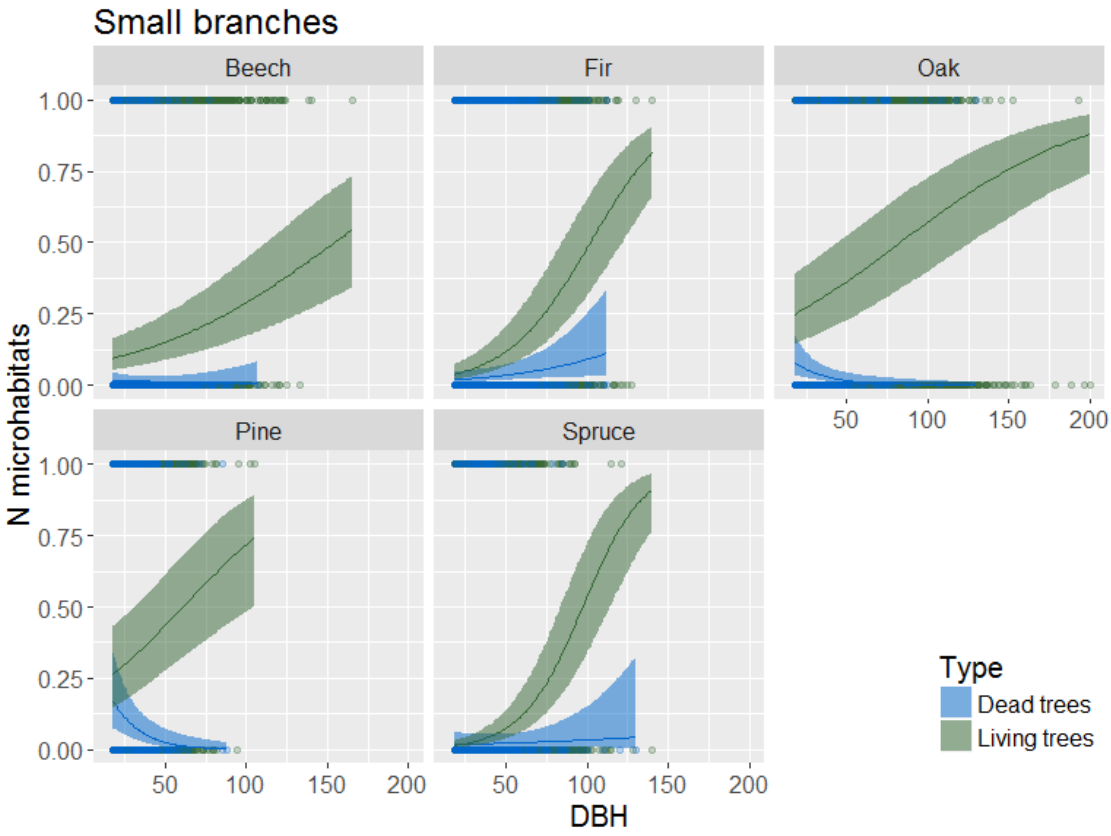

Conks of fungi
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

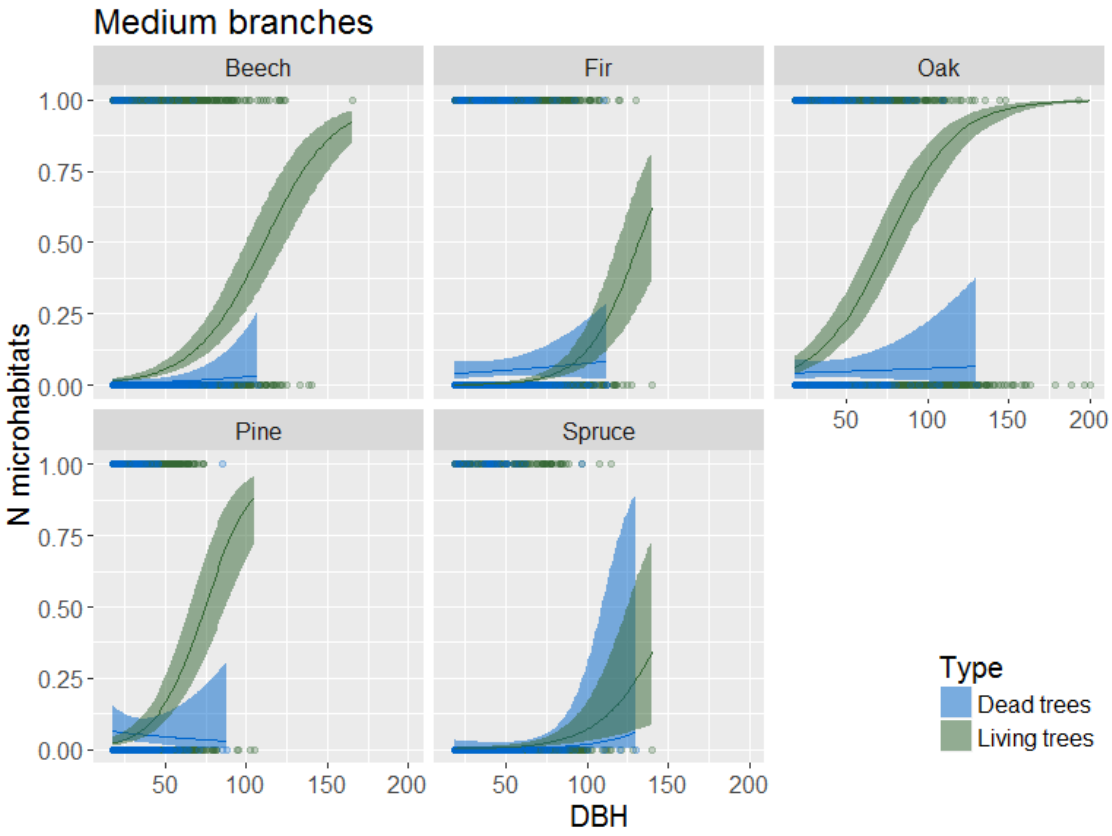

Bark characteristics
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

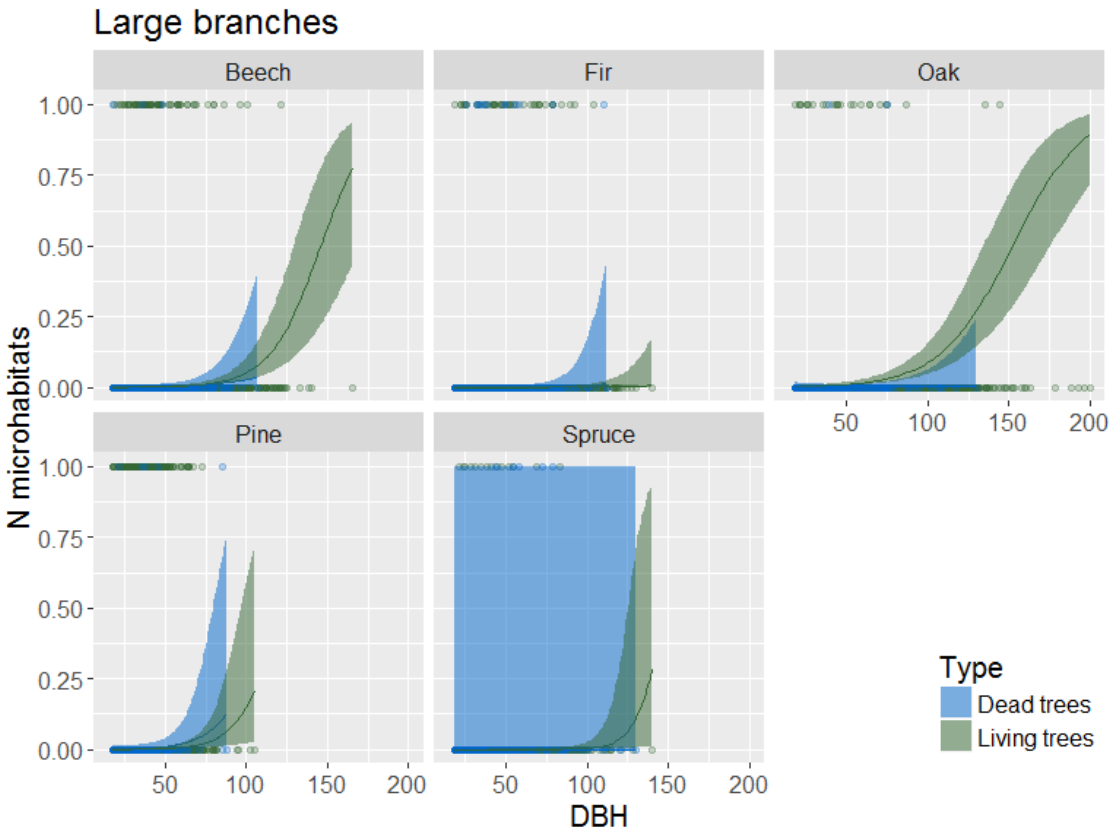

Moss cover >50%
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

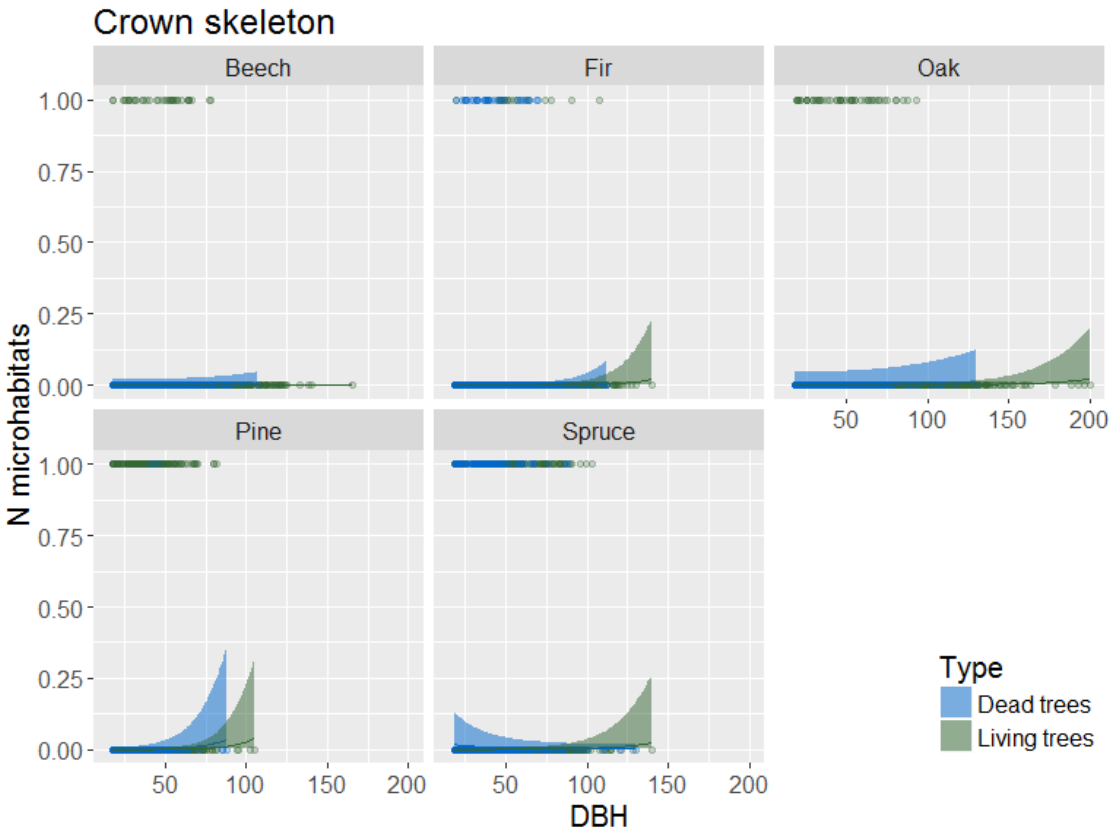

Lichen cover >50%
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

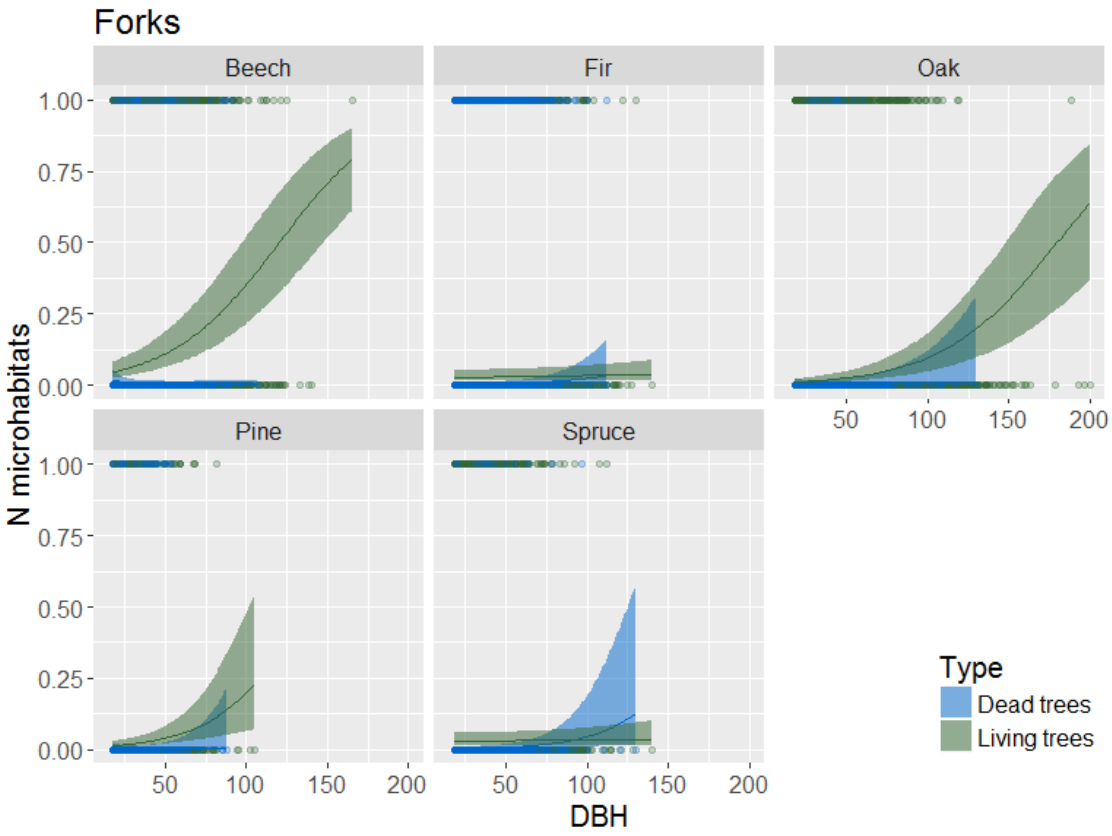

Ivy cover >50%
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

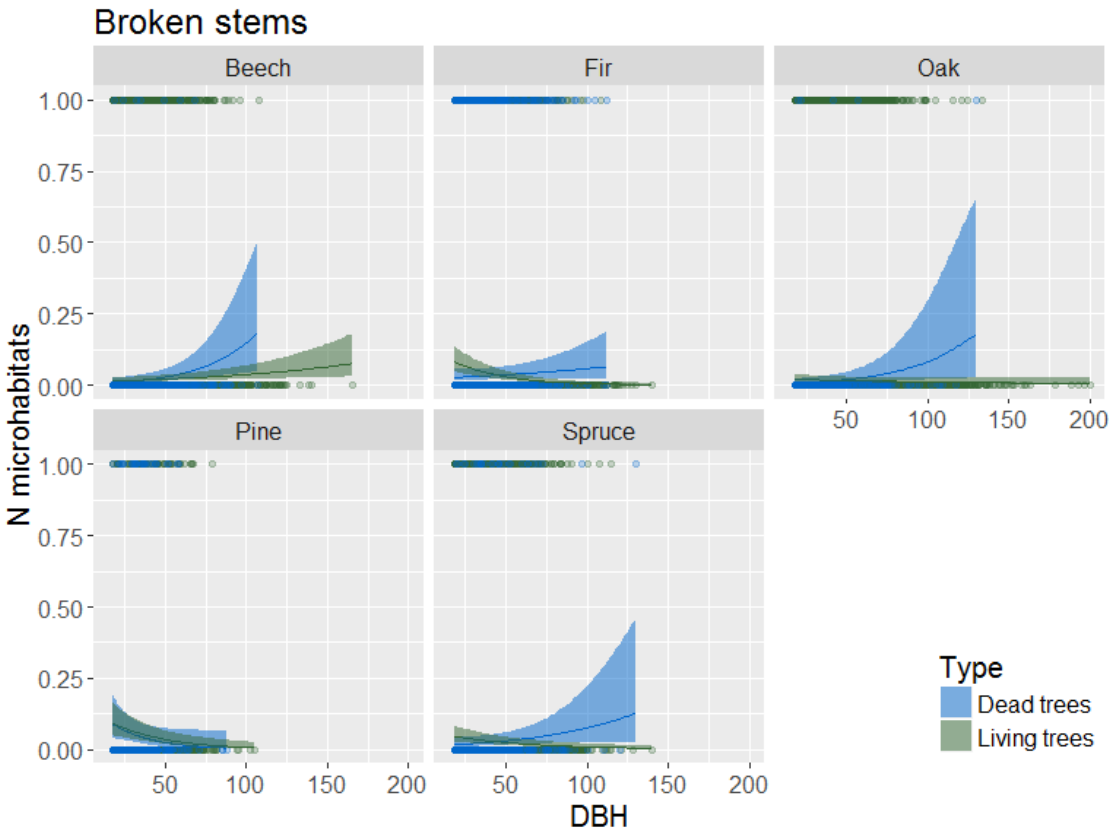

Small branches
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Medium branches
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Large branches
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Crown skeleton
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Forks
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees


Broken stems
Beech
Fir
Oak
Pine
Spruce
N microhabitats
1.00
0.75
0.50
0.25
0.00
50
100
150
200
DBH
Type
Dead trees
Living trees

Annexes C : Snags and large trees drive higher tree microhabitat densities in strict forest reserves – Supplementary materials

Yoan Paillet, Frédéric Archaux, Vincent Boulanger, Nicolas Debaive, Marc Fuhr, Olivier Gilg, Frédéric Gosselin, Eric Guilbert

Forest Ecology and Management 389 (2017) 176

*Annexe 8 : Comparison of microhabitat densities (ha^{-1}) between strict forest reserves (SFR, n=114) and managed (MAN, n=108) forests. mh= microhabitat; mean = posterior mean estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
All trees	Total	172.5	136.4	209.7	211.3	173.7	247.8	0.0081	**
	Broken forks	0.9	-0.6	2.5	2.6	1.0	4.1	0.0481	*
	Conks of fungi	3.3	1.5	5.1	3.1	1.3	5.0	0.9044	ns
	Woodpecker cavities	1.5	0.1	3.0	3.4	1.9	4.9	0.0394	*
	Non-woodpecker cavities	6.6	2.6	10.6	11.0	6.9	15.0	0.0224	*
	Base cavities	1.4	-0.2	3.0	3.2	1.5	4.8	0.0088	**
	Cracks	12.3	5.2	19.3	18.4	11.2	25.3	0.0114	*
	Bark characteristics	76.9	56.8	98.3	85.7	64.6	106.4	0.2351	ns
	Outgrowths	9.5	4.5	14.8	8.9	3.7	14.1	0.7284	ns
	Exudates	6.7	1.3	12.4	3.1	-2.5	8.6	0.0075	**
	Epiphytes	42.6	23.3	62.7	56.0	36.1	75.1	0.0094	**
Living trees	Total	162.6	129.4	197.9	181.4	146.0	215.1	0.1489	ns
	Very large trees	15.6	4.3	27.4	25.9	14.1	37.3	0.0050	**
	Large trees	51.8	35.7	69.4	57.8	41.0	74.7	0.3004	ns
	Medium trees	95.0	65.2	122.8	97.6	68.4	126.3	0.8154	ns
	Crown deadwood	8.5	1.7	14.9	11.9	5.3	18.6	0.1762	ns
	Broken forks	1.0	-0.6	2.4	2.2	0.8	3.8	0.1225	ns
	Conks of fungi	2.3	0.9	3.8	1.5	0.0	3.0	0.3077	ns
	Woodpecker cavities	0.9	0.0	1.9	1.7	0.7	2.7	0.1977	ns
	Non-woodpecker cavities	6.3	2.6	9.9	9.6	5.9	13.3	0.0647	(*)
	Base cavities	1.4	-0.1	2.9	2.5	0.9	4.0	0.0892	(*)
	Cracks	10.5	5.1	16.2	13.3	7.8	18.8	0.1169	ns
	Bark characteristics	72.3	53.8	89.8	72.6	54.1	90.4	0.9707	ns
	Outgrowths	9.5	4.5	14.7	8.5	3.4	13.7	0.6009	ns
	Exudates	6.7	1.4	12.4	3.0	-2.6	8.6	0.0052	**
	Epiphytes	42.3	22.8	62.3	54.2	34.1	73.2	0.0255	*
Snags	Total	9.9	-4.0	24.1	29.9	15.3	43.7	0.0001	***
	Crown skeletons	1.5	-1.0	3.9	3.5	1.1	5.9	0.0311	*
	Broken forks	0.0	-0.3	0.3	0.4	0.0	0.7	0.0481	*
	Conks of fungi	1.0	-0.2	2.1	1.7	0.5	2.8	0.2184	ns

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
	Woodpecker cavities	0.6	-0.2	1.4	1.7	0.8	2.5	0.0402	*
	Non-woodpecker cavities	0.3	-0.5	1.2	1.4	0.6	2.2	0.0047	**
	Base cavities	0.0	-0.5	0.5	0.7	0.2	1.2	0.0017	**
	Cracks	1.7	-1.1	4.4	5.0	2.3	7.8	0.0113	*
	Bark characteristics	4.6	-2.2	11.4	13.1	6.1	20.0	0.0034	**
	Outgrowths	0.0	-0.2	0.3	0.3	0.0	0.6	0.0372	*
	Exudates	0.0	-0.2	0.1	0.1	0.0	0.3	0.1441	ns
	Epiphytes	0.2	-0.7	1.1	1.9	0.9	2.8	0.0001	***
Very large trees	Crown deadwood	0.6	-0.3	1.5	1.5	0.6	2.5	0.0267	*
	Broken forks	0.2	-0.3	0.7	0.5	0.0	0.9	0.2545	ns
	Conks of fungi	0.3	-0.2	0.7	0.4	-0.1	0.8	0.5332	ns
	Woodpecker cavities	0.3	-0.1	0.7	0.6	0.1	1.0	0.2646	ns
	Non-woodpecker cavities	0.6	-0.1	1.3	1.6	0.9	2.4	0.0017	**
	Base cavities	0.3	-0.1	0.7	0.4	0.0	0.9	0.4361	ns
	Cracks	1.8	0.1	3.4	3.2	1.5	4.8	0.0213	*
	Bark characteristics	6.8	2.3	11.4	9.6	5.0	14.1	0.0444	*
	Outgrowths	1.1	-0.2	2.4	2.1	0.8	3.4	0.0274	*
	Exudates	0.5	-0.3	1.4	0.9	0.0	1.7	0.3029	ns
	Epiphytes	3.1	-0.1	6.6	5.0	1.7	8.4	0.0438	*
Large trees	Crown deadwood	2.7	0.6	5.0	3.5	1.3	5.8	0.4600	ns
	Broken forks	0.1	-0.2	0.5	0.5	0.1	0.8	0.1533	ns
	Conks of fungi	0.9	0.1	1.7	0.6	-0.2	1.4	0.5703	ns
	Woodpecker cavities	0.4	-0.2	0.9	0.8	0.2	1.3	0.2876	ns
	Non-woodpecker cavities	2.0	0.6	3.3	3.1	1.7	4.5	0.1145	ns
	Base cavities	0.5	-0.1	1.2	1.1	0.4	1.8	0.0859	(*)
	Cracks	4.5	1.9	7.1	5.6	2.9	8.2	0.2636	ns
	Bark characteristics	22.2	14.0	30.7	24.7	16.5	33.2	0.3426	ns
	Outgrowths	3.1	1.3	5.0	3.1	1.3	5.0	0.9756	ns
	Exudates	3.2	0.7	5.8	1.3	-1.3	3.9	0.0050	**
	Epiphytes	12.3	6.3	18.6	13.5	7.5	19.7	0.5271	ns
Medium trees	Crown deadwood	5.2	0.1	10.5	7.0	1.7	12.2	0.4107	ns
	Broken forks	0.7	-0.7	2.0	1.3	0.1	2.7	0.3721	ns
	Conks of fungi	1.2	0.2	2.2	0.5	-0.5	1.5	0.2557	ns
	Woodpecker cavities	0.2	-0.3	0.8	0.4	-0.1	1.0	0.6434	ns
	Non-woodpecker cavities	3.8	1.3	6.4	5.0	2.5	7.7	0.4529	ns
	Base cavities	0.6	-0.4	1.6	0.9	-0.1	1.9	0.5437	ns
	Cracks	4.2	0.2	8.2	4.6	0.6	8.6	0.7960	ns
	Bark characteristics	43.2	29.2	57.4	38.1	23.7	52.0	0.3521	ns
	Outgrowths	5.2	2.1	8.1	3.3	0.4	6.5	0.1507	ns
	Exudates	3.0	0.3	5.8	0.9	-1.9	3.6	0.0147	*
	Epiphytes	27.0	11.8	41.8	35.6	20.4	50.3	0.0544	(*)

*Annexe 9 : Comparison of microhabitat densities (ha-1) between strict forest reserves (SFR, n=70) and managed (MAN, n=65) lowland forests. mh= microhabitat; mean = posterior mean estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
All trees	Total	174.1	121.3	229.2	194.1	143.6	252.3	0.2235	ns
	Broken forks	1.7	-1.1	4.6	3.5	0.6	6.4	0.1575	ns
	Conks of fungi	4.0	1.3	7.1	3.0	0.2	6.1	0.4738	ns
	Woodpecker cavities	1.6	-0.9	4.0	4.3	1.8	6.8	0.0364	*
	Non-woodpecker cavities	6.5	0.0	13.3	9.0	2.2	15.6	0.2934	ns
	Base cavities	0.6	-1.0	2.3	1.5	-0.2	3.2	0.1675	ns
	Cracks	12.8	4.4	21.2	14.8	6.2	23.3	0.3334	ns
	Bark characteristics	69.0	47.7	90.5	67.0	45.4	88.8	0.7956	ns
	Outgrowths	8.6	1.6	15.7	9.0	2.2	16.5	0.8643	ns
	Exudates	0.3	-0.9	1.4	0.9	-0.3	2.0	0.3055	ns
	Epiphytes	56.8	20.2	93.7	64.9	26.8	101.1	0.2183	ns
Living trees	Total	170.7	112.7	227.8	177.3	121.9	238.2	0.6746	ns
	Very large trees	18.8	-5.9	42.5	27.1	2.6	52.0	0.1031	ns
	Large trees	48.3	17.1	78.5	54.2	24.2	86.6	0.4234	ns
	Medium trees	103.8	47.1	164.0	96.4	38.1	156.3	0.5782	ns
	Crown deadwood	11.3	-1.4	24.9	14.7	0.8	27.2	0.3631	ns
	Broken forks	1.7	-1.0	4.5	2.8	0.0	5.7	0.3504	ns
	Conks of fungi	3.7	1.2	6.3	2.3	-0.2	5.1	0.2924	ns
	Woodpecker cavities	1.2	-0.5	2.8	2.5	0.8	4.2	0.1519	ns
	Non-woodpecker cavities	6.5	0.4	13.0	7.7	1.4	14.1	0.6042	ns
	Base cavities	0.7	-0.7	2.3	1.0	-0.4	2.7	0.5269	ns
	Cracks	12.0	3.6	20.1	13.4	5.4	22.2	0.4788	ns
	Bark characteristics	68.0	44.0	90.4	60.6	37.1	84.2	0.2699	ns
	Outgrowths	8.5	1.6	14.9	8.6	2.2	15.7	0.9845	ns
	Exudates	0.3	-0.7	1.4	0.7	-0.3	1.7	0.5630	ns
	Epiphytes	56.7	20.3	93.6	63.4	27.7	101.7	0.3106	ns
Snags	Total	3.5	-6.4	13.6	17.1	6.8	27.0	0.0008	***
	Crown skeletons	0.7	-0.9	2.5	1.8	0.1	3.5	0.0656	(*)
	Broken forks	0.0	-0.7	0.7	0.6	-0.1	1.3	0.0413	*
	Conks of fungi	0.3	-0.6	1.3	0.7	-0.2	1.7	0.4056	ns
	Woodpecker cavities	0.5	-1.0	1.8	1.9	0.5	3.3	0.0537	(*)
	Non-woodpecker cavities	0.1	-1.1	1.4	1.3	0.0	2.6	0.0009	***
	Base cavities	-0.1	-0.6	0.4	0.4	-0.1	0.9	0.0240	*
	Cracks	0.7	-0.4	1.8	1.3	0.2	2.5	0.2219	ns
	Bark characteristics	1.3	-2.7	5.4	6.8	2.7	11.0	0.0043	**
	Outgrowths	0.1	-0.5	0.7	0.5	-0.1	1.1	0.0614	(*)
	Exudates	0.0	-0.3	0.3	0.2	-0.1	0.5	0.1348	ns
	Epiphytes	0.1	-0.9	1.0	1.5	0.5	2.5	0.0049	**
Very large trees	Crown deadwood	0.7	-1.0	2.5	2.1	0.4	3.9	0.0245	*
	Broken forks	0.4	-0.5	1.3	0.8	-0.1	1.8	0.2461	ns

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
	Conks of fungi	0.4	-0.5	1.4	0.7	-0.2	1.7	0.4542	ns
	Woodpecker cavities	0.5	-0.4	1.3	0.9	0.0	1.8	0.1973	ns
	Non-woodpecker cavities	0.7	-0.3	1.7	1.3	0.2	2.3	0.1566	ns
	Base cavities	0.1	-0.3	0.4	0.2	-0.2	0.5	0.7011	ns
	Cracks	2.6	-0.9	6.2	4.0	0.5	7.7	0.1244	ns
	Bark characteristics	7.8	-1.5	17.0	9.7	0.7	19.5	0.2901	ns
	Outgrowths	1.5	-0.9	3.8	2.1	-0.3	4.4	0.3037	ns
	Exudates	0.1	-0.2	0.3	0.1	-0.1	0.4	0.6210	ns
	Epiphytes	4.0	-3.7	11.5	5.3	-2.4	13.0	0.3078	ns
Large trees	Crown deadwood	3.3	-0.7	7.3	3.8	-0.2	7.9	0.7286	ns
	Broken forks	0.2	-0.5	0.8	0.5	-0.1	1.2	0.3424	ns
	Conks of fungi	1.5	0.1	2.9	0.8	-0.6	2.2	0.3248	ns
	Woodpecker cavities	0.5	-0.4	1.4	0.9	0.0	1.8	0.4505	ns
	Non-woodpecker cavities	1.9	-0.1	4.0	2.1	0.0	4.2	0.8415	ns
	Base cavities	0.0	-0.5	0.5	0.6	0.1	1.1	0.0396	*
	Cracks	5.6	0.4	10.7	6.0	0.8	11.2	0.7069	ns
	Bark characteristics	18.9	4.3	33.5	21.6	7.3	37.0	0.3723	ns
	Outgrowths	2.6	-0.6	5.7	3.6	0.5	7.0	0.3007	ns
	Exudates	0.1	-0.5	0.6	0.3	-0.3	0.8	0.5286	ns
	Epiphytes	13.9	2.7	24.2	14.1	3.7	25.5	0.9529	ns
Medium trees	Crown deadwood	7.4	-3.3	18.5	8.8	-2.3	19.6	0.6539	ns
	Broken forks	1.1	-1.3	3.6	1.5	-1.0	4.0	0.7511	ns
	Conks of fungi	1.7	-0.1	3.6	0.9	-1.0	2.8	0.3556	ns
	Woodpecker cavities	0.2	-0.8	1.2	0.7	-0.3	1.8	0.4076	ns
	Non-woodpecker cavities	4.0	-0.4	8.2	4.4	0.1	8.7	0.8304	ns
	Base cavities	0.7	-1.0	2.3	0.4	-1.2	2.1	0.5693	ns
	Cracks	3.7	0.0	7.6	3.3	-0.4	7.3	0.7440	ns
	Bark characteristics	41.4	19.3	62.6	29.4	7.2	51.1	0.0401	*
	Outgrowths	4.5	1.0	7.6	3.0	-0.2	6.5	0.3549	ns
	Exudates	0.2	-0.5	1.0	0.3	-0.5	1.1	0.9063	ns
	Epiphytes	38.9	10.0	68.8	44.0	15.4	74.9	0.3804	ns

*Annexe 10 : Comparison of microhabitat densities (ha-1) between managed (MAN, n=44) and strict forest reserves (SFR, n=43) mountain forests. mh= microhabitat; mean = posterior mean estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
All trees	Total	167.4	82.8	246.9	235.1	150.6	314.4	0.0146	*
	Broken forks	0.0	-1.5	1.5	1.5	0.0	3.0	0.0703	(*)
	Conks of fungi	2.2	-1.2	5.5	3.3	-0.1	6.6	0.3892	ns
	Woodpecker cavities	1.5	-0.7	3.6	2.1	0.0	4.2	0.5635	ns
	Non-woodpecker cavities	6.4	-1.3	14.3	13.7	6.1	21.5	0.0231	*
	Base cavities	2.1	-1.4	5.7	5.3	1.8	8.8	0.0300	*
	Cracks	11.1	-6.3	28.5	23.4	5.8	40.8	0.0176	*
	Bark characteristics	83.8	33.9	132.5	109.0	58.6	156.8	0.0946	(*)
	Outgrowths	10.8	-0.9	23.9	8.6	-3.9	20.9	0.4202	ns
	Exudates	15.2	0.6	28.9	5.2	-9.1	19.2	0.0020	**
	Epiphytes	25.6	-4.0	55.3	47.5	17.0	77.2	0.0114	*
Living trees	Total	151.1	82.5	222.5	189.2	116.9	257.2	0.0900	(*)
	Very large trees	11.9	-3.9	27.3	25.1	9.3	40.7	0.0075	**
	Large trees	56.1	25.7	86.8	62.1	30.7	92.2	0.5203	ns
	Medium trees	83.9	42.8	127.0	103.0	60.4	144.0	0.3031	ns
	Crown deadwood	5.0	-2.5	12.9	8.6	0.9	16.4	0.2138	ns
	Broken forks	0.0	-1.5	1.5	1.5	0.0	3.0	0.0703	(*)
	Conks of fungi	0.5	-0.6	1.5	0.5	-0.5	1.5	0.9587	ns
	Woodpecker cavities	0.7	-0.5	1.9	0.7	-0.4	1.9	0.9387	ns
	Non-woodpecker cavities	5.6	-1.0	12.5	12.2	5.6	19.0	0.0245	*
	Base cavities	2.1	-1.3	5.7	4.2	0.7	7.7	0.1117	ns
	Cracks	8.6	-4.1	20.9	13.5	0.8	25.8	0.1231	ns
	Bark characteristics	75.9	35.8	118.4	87.9	46.4	129.0	0.3417	ns
	Outgrowths	10.8	-1.5	23.4	8.4	-4.1	20.8	0.3757	ns
	Exudates	15.2	0.6	28.9	5.2	-9.1	19.2	0.0020	**
	Epiphytes	25.2	-4.4	55.3	45.2	14.3	75.1	0.0185	*
Snags	Total	16.2	-18.3	52.3	45.9	10.5	81.4	0.0187	*
	Crown skeletons	2.2	-4.3	8.5	5.6	-0.9	12.0	0.1071	ns
	Broken forks	-	-	-	-	-	-	-	-
	Conks of fungi	1.7	-0.9	4.6	2.9	0.3	5.7	0.3552	ns
	Woodpecker cavities	0.8	-0.6	2.2	1.4	0.0	2.8	0.4045	ns
	Non-woodpecker cavities	0.7	-1.0	2.6	1.5	-0.3	3.4	0.3266	ns
	Base cavities	0.0	-1.2	1.3	1.1	-0.1	2.3	0.0201	*
	Cracks	2.4	-4.4	8.9	9.8	3.2	16.5	0.0204	*
	Bark characteristics	7.9	-9.8	24.8	21.2	3.2	38.0	0.0457	*
	Outgrowths	0.0	-0.4	0.4	0.2	-0.2	0.5	0.3096	ns
	Exudates	-	-	-	-	-	-	-	-
	Epiphytes	0.4	-1.9	2.9	2.3	-0.2	4.7	0.0177	*
Very large trees	Crown deadwood	0.5	-0.6	1.7	0.8	-0.4	1.9	0.5217	ns
	Broken forks	-	-	-	-	-	-	-	-

	Variable	Mean MAN	lw	up	Mean SFR	lw	up	p	
	Conks of fungi	0.1	-0.1	0.4	0.1	-0.2	0.3	0.7543	ns
	Woodpecker cavities	0.2	-0.2	0.6	0.2	-0.2	0.5	0.8474	ns
	Non-woodpecker cavities	0.4	-1.1	2.0	2.2	0.6	3.7	0.0014	**
	Base cavities	0.5	-0.5	1.6	0.8	-0.2	1.9	0.5067	ns
	Cracks	0.8	-0.5	2.2	2.3	1.0	3.7	0.0330	*
	Bark characteristics	5.6	-1.2	12.6	9.8	2.5	16.4	0.0553	(*)
	Outgrowths	0.5	-1.8	3.1	2.3	-0.3	4.7	0.0278	*
	Exudates	1.0	-1.3	3.3	1.8	-0.6	4.0	0.3609	ns
	Epiphytes	2.2	-0.7	5.1	4.8	1.9	7.8	0.0153	*
Large trees	Crown deadwood	1.9	-1.5	5.3	3.0	-0.3	6.5	0.4428	ns
	Broken forks	0.0	-0.4	0.5	0.4	-0.1	0.8	0.1544	ns
	Conks of fungi	0.0	-0.6	0.6	0.4	-0.1	1.1	0.1779	ns
	Woodpecker cavities	0.2	-0.7	1.1	0.6	-0.3	1.5	0.4087	ns
	Non-woodpecker cavities	1.9	-0.8	4.6	4.5	1.8	7.2	0.0359	*
	Base cavities	1.1	-0.5	2.8	1.7	0.1	3.4	0.4348	ns
	Cracks	3.2	-0.7	7.3	5.2	1.2	9.2	0.2082	ns
	Bark characteristics	26.1	10.4	40.9	28.3	12.3	42.9	0.6494	ns
	Outgrowths	4.1	0.6	7.7	2.3	-1.2	5.8	0.1957	ns
	Exudates	7.3	0.9	13.8	2.1	-4.2	8.8	0.0015	**
	Epiphytes	10.2	-1.2	22.1	13.1	1.4	25.1	0.3675	ns
Medium trees	Crown deadwood	2.5	-1.7	6.9	4.8	0.3	9.0	0.2490	ns
	Broken forks	0.0	-1.4	1.4	1.1	-0.3	2.5	0.1497	ns
	Conks of fungi	0.4	-0.3	1.1	0.0	-0.7	0.7	0.3273	ns
	Woodpecker cavities	0.3	-0.3	0.8	0.0	-0.6	0.5	0.3428	ns
	Non-woodpecker cavities	3.4	-1.2	8.1	5.6	0.8	10.1	0.3248	ns
	Base cavities	0.5	-1.8	2.7	1.7	-0.5	4.1	0.2459	ns
	Cracks	4.7	-5.7	15.7	6.1	-4.5	16.9	0.5762	ns
	Bark characteristics	44.4	15.9	73.5	50.1	20.1	78.1	0.5910	ns
	Outgrowths	6.2	-1.4	14.0	3.7	-4.0	11.4	0.2498	ns
	Exudates	6.8	-0.5	14.0	1.4	-6.0	8.5	0.0080	**
	Epiphytes	13.2	-5.7	30.1	27.5	9.7	45.7	0.0387	*

*Annexe 11 : Effects of time since last harvesting on microhabitat densities (n=187). mh= microhabitat. Posterior mean intercepts and slopes are estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value tested vs the null hypothesis (slope = 0); ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; sup.50 = % of variation for 50 years; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
All trees	Total	170.94	125.84	216.01	0.64	0.12	1.16	0.0147	*	18.7
	Broken forks	0.52	-1.33	2.39	0.05	0.02	0.08	0.0004	***	480.8
	Conks of fungi	4.07	2.03	6.11	-0.01	-0.04	0.03	0.6082	ns	-12.3
	Woodpecker cavities	0.64	-0.88	2.03	0.07	0.04	0.10	0.0001	***	546.9
	Non-woodpecker cavities	7.65	3.17	12.02	0.05	-0.02	0.12	0.1463	ns	32.7
	Base cavities	0.95	-1.10	2.96	0.04	0.02	0.06	0.0008	***	210.5
	Cracks	12.04	3.71	20.92	0.14	0.06	0.23	0.0020	**	58.1
	Bark characteristics	69.92	45.46	94.99	0.25	-0.01	0.51	0.0617	(*)	17.9
	Outgrowths	7.89	3.40	12.26	-0.01	-0.06	0.05	0.8428	ns	-6.3
	Exudates	1.20	-1.21	3.63	0.02	-0.01	0.04	0.1783	ns	83.3
	Epiphytes	54.50	29.59	78.36	-0.02	-0.21	0.19	0.8845	ns	-1.8
Living trees	Total	165.85	125.06	204.54	0.04	-0.42	0.50	0.8496	ns	1.2
	Very large trees	14.90	0.35	28.29	0.13	-0.01	0.26	0.0545	(*)	43.6
	Large trees	49.29	28.72	68.54	0.13	-0.08	0.34	0.2200	ns	13.2
	Medium trees	101.04	67.80	133.51	-0.20	-0.58	0.17	0.2999	ns	-9.9
	Crown deadwood	10.12	2.19	18.19	0.02	-0.07	0.11	0.6934	ns	9.9
	Broken forks	0.68	-1.12	2.50	0.04	0.01	0.07	0.0086	**	294.1
	Conks of fungi	3.00	1.32	4.60	-0.02	-0.05	0.01	0.1272	ns	-33.3
	Woodpecker cavities	0.39	-0.67	1.38	0.04	0.02	0.06	0.0003	***	512.8
	Non-woodpecker cavities	7.84	3.69	12.09	0.01	-0.06	0.08	0.7388	ns	6.4
	Base cavities	1.29	-0.57	3.13	0.02	-0.01	0.04	0.1450	ns	77.5
	Cracks	10.37	3.39	16.79	0.06	-0.01	0.12	0.0670	(*)	28.9
	Bark characteristics	68.00	47.62	89.13	-0.02	-0.24	0.20	0.8406	ns	-1.5
	Outgrowths	7.79	3.55	11.84	-0.01	-0.07	0.05	0.6896	ns	-6.4
	Exudates	1.27	-1.18	3.73	0.01	-0.01	0.04	0.2814	ns	39.4
	Epiphytes	54.65	29.87	78.29	-0.06	-0.26	0.14	0.5683	ns	-5.5
Snags	Total	5.13	-11.19	21.77	0.59	0.41	0.78	0.0001	***	575.0
	Crown skeletons	1.20	-1.57	4.20	0.06	0.03	0.10	0.0003	***	250.0
	Broken forks	-0.15	-0.54	0.24	0.01	0.01	0.02	0.0004	***	333.3
	Conks of fungi	1.08	-0.39	2.52	0.01	-0.01	0.03	0.1644	ns	46.3
	Woodpecker cavities	0.26	-0.60	1.09	0.03	0.01	0.05	0.0003	***	576.9
	Non-woodpecker cavities	-0.15	-1.10	0.84	0.04	0.03	0.05	0.0001	***	1333.3
	Base cavities	-0.32	-0.88	0.24	0.02	0.02	0.03	0.0001	***	312.5
	Cracks	1.39	-1.92	4.70	0.09	0.04	0.13	0.0004	***	323.7
	Bark characteristics	1.89	-5.99	9.93	0.27	0.17	0.37	0.0001	***	714.3
	Outgrowths	0.12	-0.30	0.54	0.00	0.00	0.01	0.0614	(*)	0.0
	Exudates	-0.03	-0.22	0.14	0.00	0.00	0.01	0.0510	(*)	0.0
	Epiphytes	-0.08	-1.28	1.09	0.04	0.03	0.06	0.0001	***	2500.0
Very large trees	Crown deadwood	0.28	-0.79	1.30	0.02	0.01	0.04	0.0008	***	357.1

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
	Broken forks	-0.11	-0.64	0.42	0.02	0.01	0.02	0.0003	***	909.1
	Conks of fungi	0.29	-0.28	0.82	0.00	0.00	0.01	0.4428	ns	0.0
	Woodpecker cavities	0.28	-0.17	0.73	0.01	0.00	0.02	0.0344	*	178.6
	Non-woodpecker cavities	0.49	-0.15	1.15	0.01	0.00	0.02	0.0140	*	102.0
	Base cavities	0.19	-0.27	0.65	0.00	0.00	0.01	0.4502	ns	0.0
	Cracks	2.19	0.03	4.27	0.01	-0.01	0.03	0.2852	ns	22.8
	Bark characteristics	6.26	1.12	11.43	0.03	-0.02	0.08	0.2724	ns	24.0
	Outgrowths	1.24	-0.34	2.81	0.01	-0.01	0.02	0.4930	ns	40.3
	Exudates	0.23	-0.19	0.62	0.00	-0.01	0.01	0.5916	ns	0.0
	Epiphytes	3.87	-0.38	7.88	0.01	-0.03	0.05	0.6029	ns	12.9
Large trees	Crown deadwood	2.44	-0.03	4.96	0.02	-0.01	0.05	0.2592	ns	41.0
	Broken forks	-0.14	-0.52	0.24	0.02	0.01	0.02	0.0002	***	714.3
	Conks of fungi	1.15	0.27	2.03	-0.01	-0.02	0.01	0.3706	ns	-43.5
	Woodpecker cavities	0.00	-0.59	0.57	0.02	0.01	0.03	0.0003	***	5000.0
	Non-woodpecker cavities	1.92	0.52	3.33	0.02	-0.01	0.04	0.1678	ns	52.1
	Base cavities	0.71	-0.12	1.58	0.01	-0.01	0.02	0.3901	ns	70.4
	Cracks	4.32	0.83	7.45	0.02	-0.01	0.06	0.1931	ns	23.1
	Bark characteristics	21.28	11.64	30.74	0.05	-0.04	0.14	0.3426	ns	11.7
	Outgrowths	2.84	0.87	4.87	0.00	-0.02	0.03	0.9296	ns	0.0
	Exudates	0.25	-0.69	1.19	0.01	0.00	0.02	0.0307	*	200.0
	Epiphytes	14.72	7.33	21.76	-0.02	-0.10	0.05	0.5364	ns	-6.8
Medium trees	Crown deadwood	7.53	0.79	14.29	-0.03	-0.10	0.05	0.5047	ns	-19.9
	Broken forks	1.03	-0.54	2.59	0.01	-0.02	0.03	0.6534	ns	48.5
	Conks of fungi	1.54	0.35	2.65	-0.02	-0.04	0.00	0.1043	ns	-64.9
	Woodpecker cavities	0.12	-0.55	0.75	0.01	0.00	0.02	0.1458	ns	416.7
	Non-woodpecker cavities	5.20	1.87	8.32	-0.01	-0.06	0.05	0.7821	ns	-9.6
	Base cavities	0.44	-0.58	1.52	0.01	-0.01	0.02	0.5063	ns	113.6
	Cracks	3.91	-1.12	8.91	0.02	-0.02	0.07	0.3075	ns	25.6
	Bark characteristics	40.32	24.29	56.16	-0.09	-0.27	0.09	0.3471	ns	-11.2
	Outgrowths	3.92	1.77	5.89	-0.02	-0.06	0.02	0.2982	ns	-25.5
	Exudates	0.64	-0.67	2.03	0.00	-0.01	0.02	0.7831	ns	0.0
	Epiphytes	36.39	17.29	54.64	-0.06	-0.23	0.11	0.4900	ns	-8.2

*Annexe 12 : Effects of time since last harvesting on microhabitat densities in lowland forests (n=128). mh= microhabitat. Posterior mean intercepts and slopes are estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value tested vs the null hypothesis (slope = 0); ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; sup.50 = % of variation for 50 years; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
All trees	Total	180.06	124.90	237.16	0.20	-0.31	0.72	0.4384	ns	5.6
	Broken forks	1.19	-1.55	3.96	0.06	0.02	0.10	0.0022	**	252.1
	Conks of fungi	4.05	1.21	7.04	-0.01	-0.05	0.03	0.6648	ns	-12.3
	Woodpecker cavities	0.74	-1.32	2.66	0.09	0.05	0.13	0.0000	***	608.1
	Non-woodpecker cavities	7.28	1.03	13.97	0.03	-0.05	0.11	0.4088	ns	20.6
	Base cavities	-0.23	-0.92	0.41	0.03	0.02	0.05	0.0000	***	652.2
	Cracks	12.23	2.54	22.36	0.04	-0.03	0.11	0.2338	ns	16.4
	Bark characteristics	64.39	39.99	87.75	0.00	-0.21	0.22	0.9647	ns	0.0
	Outgrowths	9.94	1.59	17.58	0.00	-0.07	0.07	0.9495	ns	0.0
	Exudates	0.37	-0.81	1.44	0.01	-0.01	0.03	0.2940	ns	135.1
	Epiphytes	65.53	23.51	107.21	-0.01	-0.22	0.21	0.8939	ns	-0.8
Living trees	Total	176.46	115.18	230.91	-0.10	-0.58	0.38	0.6676	ns	-2.8
	Very large trees	19.31	-5.72	45.64	0.18	0.01	0.34	0.0340	*	46.6
	Large trees	50.94	16.99	81.68	0.09	-0.14	0.33	0.4454	ns	8.8
	Medium trees	106.17	53.31	162.81	-0.36	-0.75	0.05	0.0747	(*)	-17.0
	Crown deadwood	15.11	-0.04	29.62	-0.02	-0.13	0.10	0.7624	ns	-6.6
	Broken forks	1.27	-1.58	4.06	0.04	0.00	0.08	0.0297	*	157.5
	Conks of fungi	3.91	1.29	6.37	-0.02	-0.07	0.01	0.2120	ns	-25.6
	Woodpecker cavities	0.44	-1.04	1.78	0.05	0.03	0.08	0.0000	***	568.2
	Non-woodpecker cavities	7.29	0.78	13.77	0.00	-0.07	0.08	0.9814	ns	0.0
	Base cavities	0.00	-0.55	0.54	0.02	0.01	0.03	0.0002	***	5000.0
	Cracks	11.29	2.05	20.89	0.03	-0.04	0.09	0.3940	ns	13.3
	Bark characteristics	63.06	37.32	85.51	-0.13	-0.32	0.07	0.1802	ns	-10.3
	Outgrowths	9.67	1.98	16.79	-0.01	-0.08	0.07	0.8782	ns	-5.2
	Exudates	0.40	-0.63	1.43	0.01	-0.01	0.02	0.5445	ns	125.0
	Epiphytes	65.51	23.56	107.01	-0.04	-0.24	0.17	0.6898	ns	-3.1
Snags	Total	3.07	-5.75	12.70	0.31	0.20	0.43	0.0000	***	504.9
	Crown skeletons	1.32	-0.99	3.61	0.01	-0.01	0.02	0.4420	ns	37.9
	Broken forks	-0.11	-0.78	0.54	0.02	0.01	0.03	0.0001	***	909.1
	Conks of fungi	0.18	-0.82	1.14	0.02	0.00	0.03	0.0365	*	555.6
	Woodpecker cavities	0.29	-0.99	1.57	0.04	0.01	0.06	0.0006	***	689.7
	Non-woodpecker cavities	0.06	-1.45	1.51	0.03	0.02	0.04	0.0000	***	2500.0
	Base cavities	-0.23	-0.61	0.12	0.02	0.01	0.02	0.0000	***	434.8
	Cracks	0.85	-0.55	2.29	0.01	0.00	0.03	0.1160	ns	58.8
	Bark characteristics	0.70	-2.47	3.77	0.14	0.08	0.19	0.0000	***	1000.0
	Outgrowths	0.28	-0.57	1.10	0.00	0.00	0.01	0.3566	ns	0.0
	Exudates	-0.03	-0.32	0.25	0.01	0.00	0.01	0.0483	*	1666.7
	Epiphytes	0.14	-0.83	1.08	0.03	0.01	0.04	0.0006	***	1071.4
Very large trees	Crown deadwood	0.62	-0.98	2.23	0.03	0.01	0.05	0.0005	***	241.9

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
	Broken forks	-0.01	-0.77	0.71	0.02	0.01	0.04	0.0000	***	10000.0
	Conks of fungi	0.45	-0.59	1.45	0.00	0.00	0.01	0.3076	ns	0.0
	Woodpecker cavities	0.31	-0.50	1.08	0.01	0.00	0.02	0.0049	**	161.3
	Non-woodpecker cavities	0.56	-0.42	1.62	0.02	0.00	0.03	0.0103	*	178.6
	Base cavities	-0.04	-0.35	0.26	0.01	0.00	0.01	0.0200	*	1250.0
	Cracks	3.06	-0.83	7.09	0.02	-0.01	0.05	0.1833	ns	32.7
	Bark characteristics	7.93	-1.48	17.74	0.04	-0.02	0.10	0.1931	ns	25.2
	Outgrowths	1.90	-1.14	4.94	0.01	-0.01	0.02	0.4436	ns	26.3
	Exudates	0.06	-0.19	0.30	0.00	0.00	0.01	0.3167	ns	0.0
	Epiphytes	4.41	-3.43	12.54	0.02	-0.03	0.06	0.4424	ns	22.7
Large trees	Crown deadwood	3.24	-0.66	7.23	0.02	-0.02	0.06	0.3432	ns	30.9
	Broken forks	-0.09	-0.68	0.46	0.02	0.01	0.03	0.0001	***	1111.1
	Conks of fungi	1.46	0.02	2.87	-0.01	-0.03	0.01	0.4774	ns	-34.2
	Woodpecker cavities	0.11	-0.72	0.89	0.02	0.01	0.04	0.0006	***	909.1
	Non-woodpecker cavities	1.74	-0.14	3.83	0.02	-0.01	0.04	0.2636	ns	57.5
	Base cavities	0.05	-0.47	0.59	0.01	0.00	0.02	0.0158	*	1000.0
	Cracks	5.28	-0.41	10.89	0.02	-0.02	0.06	0.3246	ns	18.9
	Bark characteristics	20.86	5.64	36.62	0.00	-0.09	0.10	0.9182	ns	0.0
	Outgrowths	3.63	-0.01	7.03	-0.01	-0.04	0.03	0.6624	ns	-13.8
	Exudates	-0.03	-0.55	0.48	0.01	0.00	0.02	0.1142	ns	1666.7
	Epiphytes	14.59	3.15	25.32	0.00	-0.08	0.08	0.9277	ns	0.0
Medium trees	Crown deadwood	11.35	-2.13	24.75	-0.07	-0.17	0.03	0.1884	ns	-30.8
	Broken forks	1.40	-1.16	4.03	0.00	-0.04	0.03	0.9564	ns	0.0
	Conks of fungi	1.96	0.04	3.87	-0.02	-0.05	0.01	0.1478	ns	-51.0
	Woodpecker cavities	0.07	-0.92	1.06	0.02	0.00	0.03	0.0750	(*)	1428.6
	Non-woodpecker cavities	4.87	0.15	9.55	-0.02	-0.09	0.04	0.5031	ns	-20.5
	Base cavities	-	-	-	-	-	-	-	-	-
	Cracks	3.14	-0.30	6.34	-0.01	-0.05	0.02	0.4532	ns	-15.9
	Bark characteristics	34.50	16.95	51.02	-0.17	-0.33	0.00	0.0350	*	-24.6
	Outgrowths	4.30	0.88	7.55	-0.01	-0.06	0.04	0.7101	ns	-11.6
	Exudates	0.37	-0.44	1.12	0.00	-0.02	0.01	0.6079	ns	0.0
	Epiphytes	46.94	8.07	81.92	-0.06	-0.23	0.13	0.5149	ns	-6.4

*Annexe 13 : Effects of time since last harvesting on microhabitat densities in mountain forests (n=59). mh= microhabitat; Posterior mean intercepts and slopes are estimated by a linear mixed model with Gaussian error distribution fitted within a Bayesian framework using Markov Chain Monte Carlo methods. lw and up = lower and upper limits of 95% credibility intervals; p = sampled posterior Bayesian p-value tested vs the null hypothesis (slope = 0); ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result; sup.50 = % of variation for 50 years; DBH = Diameter at Breast Height. Very large trees: DBH ≥ 67.5cm; large trees: 47.5 ≤ DBH < 67.5cm; medium trees: 30 ≤ DBH < 47.5cm.*

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
All trees	Total	106.27	-89.91	282.66	2.30	0.84	3.78	0.0016	**	108.2
	Broken forks	-0.77	-4.76	2.67	0.04	0.00	0.09	0.0461	*	259.7
	Conks of fungi	3.38	-3.74	10.00	0.01	-0.07	0.08	0.8977	ns	14.8
	Woodpecker cavities	0.86	-2.89	4.91	0.03	-0.02	0.08	0.1993	ns	174.4
	Non-woodpecker cavities	7.97	-6.20	22.43	0.08	-0.09	0.24	0.3228	ns	50.2
	Base cavities	2.11	-7.88	10.28	0.06	-0.03	0.15	0.1673	ns	142.2
	Cracks	0.81	-36.63	32.17	0.51	0.22	0.79	0.0001	***	3148.1
	Bark characteristics	57.22	-26.92	140.29	1.01	0.19	1.77	0.0108	*	88.3
	Outgrowths	4.38	-3.06	11.29	0.00	-0.09	0.09	0.9686	ns	0.0
	Exudates	1.78	-8.09	11.84	0.05	-0.04	0.13	0.2644	ns	140.4
	Epiphytes	38.26	-28.40	94.35	0.02	-0.50	0.56	0.9266	ns	2.6
Living trees	Total	131.20	-5.66	257.35	0.65	-0.60	1.82	0.2735	ns	24.8
	Very large trees	13.29	-3.33	27.76	-0.04	-0.22	0.15	0.6344	ns	-15.0
	Large trees	39.15	-24.85	97.55	0.34	-0.16	0.84	0.1647	ns	43.4
	Medium trees	79.23	-8.38	160.03	0.35	-0.56	1.27	0.4211	ns	22.1
	Crown deadwood	-0.88	-13.42	10.18	0.15	0.02	0.28	0.0177	*	852.3
	Broken forks	-0.77	-4.76	2.67	0.04	0.00	0.09	0.0461	*	259.7
	Conks of fungi	0.83	-1.26	2.83	-0.01	-0.03	0.02	0.6385	ns	-60.2
	Woodpecker cavities	0.51	-2.13	3.08	0.01	-0.02	0.05	0.4753	ns	98.0
	Non-woodpecker cavities	9.11	-2.58	22.76	0.01	-0.14	0.16	0.8541	ns	5.5
	Base cavities	3.53	-3.97	10.65	0.01	-0.07	0.08	0.8890	ns	14.2
	Cracks	5.08	-16.85	27.93	0.18	0.00	0.36	0.0420	*	177.2
	Bark characteristics	66.52	-4.89	136.27	0.30	-0.37	0.97	0.3624	ns	22.5
	Outgrowths	4.69	-2.25	11.15	-0.01	-0.09	0.08	0.7798	ns	-10.7
	Exudates	1.78	-8.09	11.84	0.05	-0.04	0.13	0.2644	ns	140.4
	Epiphytes	40.94	-22.39	93.21	-0.09	-0.60	0.44	0.7149	ns	-11.0
Snags	Total	-24.76	-124.27	60.82	1.65	1.02	2.31	0.0002	***	333.2
	Crown skeletons	-4.48	-19.25	8.13	0.25	0.14	0.37	0.0002	***	279.0
	Broken forks	-	-	-	-	-	-	-	-	-
	Conks of fungi	2.71	-3.41	8.19	0.01	-0.06	0.08	0.8123	ns	18.5
	Woodpecker cavities	0.34	-1.63	2.41	0.02	-0.01	0.05	0.1407	ns	294.1
	Non-woodpecker cavities	-1.31	-5.72	2.28	0.07	0.03	0.11	0.0001	***	267.2
	Base cavities	-1.47	-5.23	1.73	0.05	0.03	0.08	0.0002	***	170.1
	Cracks	-2.98	-19.90	12.02	0.29	0.12	0.48	0.0003	***	486.6
	Bark characteristics	-10.61	-57.30	29.63	0.74	0.39	1.10	0.0002	***	348.7
	Outgrowths	-0.28	-1.17	0.52	0.01	0.00	0.02	0.0178	*	178.6
	Exudates	-	-	-	-	-	-	-	-	-
	Epiphytes	-2.64	-10.50	4.34	0.11	0.07	0.15	0.0002	***	208.3
Very large trees	Crown deadwood	0.10	-0.89	1.00	0.01	-0.01	0.02	0.3698	ns	500.0

	Variable	Mean intercept	lw	up	Mean slope	lw	up	p		sup.50
	Broken forks	-	-	-	-	-	-	-	-	-
	Conks of fungi	0.12	-0.33	0.55	0.00	-0.01	0.00	0.6172	ns	0.0
	Woodpecker cavities	0.55	-0.25	1.40	-0.01	-0.02	0.00	0.1608	ns	-90.9
	Non-woodpecker cavities	0.52	-1.13	2.28	0.00	-0.01	0.02	0.6333	ns	0.0
	Base cavities	0.80	-1.22	2.73	-0.01	-0.03	0.01	0.4603	ns	-62.5
	Cracks	1.35	-0.56	3.19	-0.01	-0.03	0.02	0.5818	ns	-37.0
	Bark characteristics	4.79	-3.13	11.98	-0.01	-0.09	0.08	0.8588	ns	-10.4
	Outgrowths	0.53	-0.96	1.97	0.00	-0.02	0.02	0.8130	ns	0.0
	Exudates	0.50	-1.45	2.43	0.00	-0.02	0.03	0.8707	ns	0.0
	Epiphytes	3.88	-1.83	8.62	-0.02	-0.07	0.04	0.4849	ns	-25.8
Large trees	Crown deadwood	0.84	-5.24	7.06	0.03	-0.05	0.10	0.4788	ns	178.6
	Broken forks	-0.23	-0.94	0.42	0.01	0.00	0.02	0.0178	*	217.4
	Conks of fungi	0.33	-1.00	1.62	0.00	-0.02	0.02	0.9223	ns	0.0
	Woodpecker cavities	-0.42	-2.64	1.47	0.02	0.00	0.05	0.0372	*	238.1
	Non-woodpecker cavities	1.88	-3.18	6.42	0.02	-0.03	0.07	0.3465	ns	53.2
	Base cavities	2.24	-0.88	5.35	-0.01	-0.05	0.02	0.4304	ns	-22.3
	Cracks	2.04	-5.87	10.12	0.04	-0.03	0.12	0.2194	ns	98.0
	Bark characteristics	17.17	-9.40	42.67	0.20	-0.06	0.43	0.0987	(*)	58.2
	Outgrowths	0.48	-5.00	5.22	0.04	-0.01	0.09	0.1403	ns	416.7
	Exudates	0.30	-3.68	4.19	0.03	-0.01	0.06	0.0976	(*)	500.0
	Epiphytes	15.77	-7.22	35.56	-0.07	-0.25	0.11	0.4259	ns	-22.2
Medium trees	Crown deadwood	-1.55	-9.04	4.51	0.11	0.03	0.19	0.0023	**	354.8
	Broken forks	-0.47	-4.09	2.68	0.03	-0.01	0.08	0.1251	ns	319.1
	Conks of fungi	0.39	-1.03	1.93	0.00	-0.02	0.02	0.6623	ns	0.0
	Woodpecker cavities	0.34	-0.89	1.50	0.00	-0.02	0.01	0.6172	ns	0.0
	Non-woodpecker cavities	6.65	-3.71	18.60	-0.02	-0.15	0.11	0.8228	ns	-15.0
	Base cavities	0.77	-4.51	5.64	0.02	-0.04	0.09	0.5140	ns	129.9
	Cracks	1.79	-19.23	21.79	0.14	-0.01	0.29	0.0592	(*)	391.1
	Bark characteristics	44.23	-6.38	99.14	0.12	-0.46	0.66	0.6460	ns	13.6
	Outgrowths	3.40	-1.12	8.07	-0.04	-0.10	0.02	0.1735	ns	-58.8
	Exudates	1.11	-4.93	7.22	0.01	-0.04	0.06	0.6269	ns	45.0
	Epiphytes	23.86	-15.58	55.72	-0.05	-0.46	0.36	0.7602	ns	-10.5

Annexes D : The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles – Supplementary materials

Yoan Paillet, Frédéric Archaux, Solène du Puy, Christophe Bouget, Vincent Boulanger, Nicolas Debaive, Olivier Gilg, Frédéric Gosselin, Eric Guilbert

Journal of Applied Ecology (2018) 1-13

Annexe 14 : Elements of methodology

Study sites selection

We compared fifteen strict forest reserves distributed across France with adjacent managed forests under the same site conditions (the sampling design is detailed in Paillet et al. 2015b, and only the main points are mentioned here). We restricted our study to mixed lowland oak-beech-hornbeam forests (*Quercus robur* L. and *Q. petraea* (Mattus.) Liebl., *Fagus sylvatica* L. and *Carpinus betulus* L., elevation ≤ 800m) and mountain beech-fir-spruce forests (*Fagus sylvatica* L., *Abies alba* Mill. and *Picea abies* (L.) Karst., elevation > 800m).

At each of the fifteen study sites, sampling locations were randomly pre-selected on a regular 100x100m grid, then plots were selected according to site conditions observed in the field. Edaphic conditions (soil texture, depth, hydromorphy and reaction to HCl) and topography (elevation, aspect and slope) were checked in the field so that each plot within the forest reserve had its paired equivalent outside the reserve. The managed plots were selected within 5km of the forest reserve boundaries and in stands composed exclusively of native tree species of the same forest type (oak-beech-hornbeam in lowlands, beech-fir-spruce in mountains). The majority of the plots were located in mature forests (see Paillet et al. 2015).

For 189 plots, the time since last harvest was recorded from management plans or wood sales data. Stand age was generally unavailable. The mean time since last harvest for the unmanaged forests was 47 years (46 +/- SD 41 years in lowlands, and 49 +/- SD 38 years in mountains) and for managed forests, 9 years (7 +/- SD 6 years in lowlands and 13 +/- SD 18 years in mountains); however, a few plots in the strict reserves may have experienced harvesting recently before designation, while a few plots in the managed forests may not have been harvested for more than 20 years.

Silvicultural treatments were also recorded even though they were strongly biased by elevation: 78% of the uneven-aged forests (continuous cover management) were located in mountain beech-fir-spruce forests whereas all the even-aged high forests (selective cutting followed by clearcutting and natural regeneration) were located in lowland beech-oak dominated forests. No other type of management (*e.g.* grazing) occurred in our plots. As a consequence of this confusion between elevation and silvicultural treatment, we did not address silvicultural treatments in our analyses (see discussion in Paillet et al. 2015b).

Microhabitat inventories

We visually inspected for microhabitats all living trees (DBH ≥ 30cm) comprised within a fixed 2% relascopic angle in lowlands (resp. 3% in mountains) and standing dead trees (*i.e.* snags with DBH ≥ 30cm, excluding stumps with a height ≤ 1 m) comprised within a 20m radius from the plot center (Paillet et al. 2015b, 2017). We recorded the presence of 28 microhabitat types based on the list

published by Vuidot et al. (2011, Table S1.1). To limit potential observer bias (Paillet et al., 2015a), all censuses were performed by one and the same observer (Y.P.), except for one site (F.G.).

Table S1.1: Microhabitat types and groupings (based on Vuidot et al. 2011).

Microhabitat types	Microhabitat groups
1. Presence of a crown skeleton (snags only)	Crown skeletons
2. Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown	Crown deadwood
3. Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown	
4. >50% of dead crown: one or more main branches are dead. The living crown appears to be <50% of the former total crown	
5. Broken stem: the primary crown is totally absent with or without the presence of a secondary crown. Main parts of the tree stem are already dead and decomposing	Broken tops
6. Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch has resulted in severe damage to the main stem	
7. Splintered stem: splitting has resulted in numerous slabs (minimum 5) of wood >50 cm long	
8. Conks of fungi. Fruiting bodies, diameter > 5cm.	Conks of fungi
9. Conks of fungi. Equal to or more than 3 fruiting bodies >5 cm in diameter	
10. Conks of fungi occurring in 10 cm long cascades of small fruiting bodies	
11. Non-woodpecker cavities with >5cm aperture: formed after injury, branch fall.	Non-woodpecker cavities
12. Woodpecker cavities with >2 cm aperture.	Woodpecker cavities
13. Cavity string: at least three woodpecker cavities on a same stem with a maximum distance of two meters between two cavity entrances	
14. Deep stem cavities: a tubular cavity in the base of the tree.	Base cavities
15. Deep stem cavities: a tubular cavity in the base of the tree with mould.	
16. Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	Cracks
17. Cracks: cleft in the sapwood >25 cm long along the stem and at least 2 cm deep	
18. Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 cm × 5 cm × 2 cm	Bark characteristics
19. Bark pocket with mould: same structure and size as 17. but with mould	
20. Bark loss: patches with bark loss of at least 5 cm × 5 cm mainly caused by injuries sustained from felling or natural falling of other trees	
21. Bark burst: black burst of bark often with resin indicating injury/disease	
22. Recent wood injury	
23. Canker: proliferation of cell growth; irregular cellular growth on stems or branches, caused by bark-inhabiting fungi, viruses or bacteria. Only cankerous areas >10 cm in diameter were recorded	Outgrowth
24. Witch broom: dense agglomeration of branches from a parasite or epicormic branching.	
25. Heavy sap or resin: fresh, heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size	Exudates
26. Sap or resin drop: Only a few sap or resin drops indicating a minor injury	
27. Bryophytes developed on >50% of the base (height <1m), trunk or branch area (noted separately)	Epiphytes
28. Ivy growing on >50% of the base (height <1m), trunk or branch area (noted separately)	

Biodiversity censuses

Bats were recorded by their echolocation calls (heterodyne and time expansion). Pettersson D980 and D240x detectors were used, associated with portable Marantz PMD620 digital recorders. Unknown and unsure heterodyne signals were analysed with Batsound 3.31 software (Barataud 2012). For each species, bat activity was assessed in terms of number of contacts per minute. A contact was either a single signal or a short sequence of signals over a maximum duration of 5 seconds. Each bat count was carried out by a team of two experienced chiropterologists for thirty minutes, three times the same year in April-May, June-July and August-September. Recording occurred at sunset on nights with no rain or wind and with temperatures above 5°C, when bat activity was more intense. No recording occurred within five days of a full moon since moonlight can negatively impact the amount of signalling

(Römer et al. 2010). Individuals that were only identified at genus level were not included in the analyses (this represented 130 occurrences, mostly *Myotis sp.* and *Plecotus sp.*, out of a total of 417 distributed over 121 plots).

Birds were inventoried following the French Breeding Bird Survey protocol (Jiguet et al. 2012). Each plot was surveyed twice a year, in April-May for early nesters and in May-June for late breeders. Each count lasted five minutes and took place within one to four hours after sunrise. All birds seen or heard within 100 m of the plot centre were counted. Wetland and farmland birds (<0.5% of the birds recorded) were excluded from our analyses as their habitat preferences are likely to be independent of the structural and landscape features targeted in this study. We also excluded raptors (<1% of the birds recorded) for which the point count method is inappropriate.

Different trained ornithologists and chiropterologists participated in the bird and bats counts between 2009 and 2013 (Bouvet et al. 2016), but all the plots in the same forest were sampled by the same person in a given year (so that the potential observer effect was partly embedded in forest and year, but was not confounded with our main factors of interest).

Flying saproxylic beetles were sampled with two unbaited cross-vane flight interception traps (PolytrapTM, E.I. Purpan, Toulouse, France) per plot. The traps were suspended roughly 1.5 m above the ground and set about 20 m apart, except for the Bois du Parc and Haut-Tuileau sites, where only one trap per plot was set. Active insects were collected from April to August. Saproxylic beetles, defined as those depending "during some parts of their life cycle, upon wounded or decaying woody material from living, weakened or dead trees" (Stokland et al., 2012), were identified to the lowest possible taxonomic level by trained entomologists and group specialists.

References

Barataud, M. (2012). Rapport d'étude: Fréquentation des prairies de fauche par les chiroptères en chasse dans les Alpes du Sud. p 28.

Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O. & Gosselin, F. (2016) Effects of forest structure, management and landscape on bird and bat communities. *Environmental Conservation*, 1-13.

Jiguet, F., Devictor, V., Julliard, R. & Couvet, D. (2012) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica*, **44**, 58-66.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F. & Guilbert, E. (2017) Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and Management, 389, 176-86.

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F. & Gosselin, F. (2015a) Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. Ecological Indicators, 49, 14-23.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O. & Gosselin, F. (2015b) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management*, **346**, 51-64.

Römer, H., Lang, A. & Hartbauer, M. (2010) The signaller's dilemma: A cost-benefit analysis of public and private communication. *PLoS ONE*, **5**.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012) *Biodiversity in dead wood* University Press, Cambridge, UK.

Vuidot, A., Paillet, Y., Archaux, F. & Gosselin, F. (2011) Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation, 144, 441-50.

Annexe 15 : Selection of microhabitat metrics and comparison with management and structure models based on differences in the Akaike Index Criterion corrected for small samples (Delta-AICc). The model with the lowest AICc has a Delta-AICc = 0 (in bold, grey filling). The microhabitat model with the lowest AICc is indicated by grey filling. SR: species richness; Ab: abundance.

1. Bats

		Total		Red-listed species		Forest specialists		Cavity roosters	
Explanatory variables		SR	Ab	SR	Ab	SR	Ab	SR	Ab
	Null model	4.1	2.3	**0**	3.3	1.7	3.9	5	10.2
Density	Total	6.1	4.4	2	5.3	3.7	6	6.8	12.2
	Trees w/ ≥ 3 types	5.8	3.8	0.6	5.1	2.6	4.7	6	12.3
	Living trees	6.2	4.3	2.1	4.5	3.9	5.9	7.1	11.5
	Snags	1.8	3.3	0.9	2.6	1.6	3	1.7	8.9
	Cavity	4.7	3.4	1.6	5.1	3.5	4.9	4.8	10.5
	Conk	5.6	3.2	2	5.4	3.7	5.8	6.6	12.3
	Crack	6.2	1.3	2	5.3	3.8	5.4	7	12.3
Diversity	Total	0.8	1.9	1.6	5	0.5	4.4	2.2	10.9
	Living trees	2.7	3	1.9	5.4	1.5	5.6	4.3	12.1
	Snags	1.4	0.7	1	**0**	1.9	0.6	2.1	5.8
Management abandonment		4	3.7	0.6	0.7	3.2	**0**	2.2	**0**
Basal area of large living trees		1.6	1.3	1.7	5.3	**0**	4.7	3.8	11.3
Large snag volume		**0**	**0**	1.4	3	1.1	2.7	**0**	7.5
Large log volume		4.7	1.2	2.1	4.1	3.8	4.4	5.5	8.5

2. Birds

		Total		Red-listed species		Forest specialists		Cavity nesters	
Explanatory variables		SR	Ab	SR	Ab	SR	Ab	SR	Ab
	Null model	3.9	7.9	**0**	0.2	1.8	6.1	7.2	16.7
Density	Total	3.5	6.7	1.9	2	2.4	5.1	5	10.8
	Trees w/ ≥ 3 types	3.3	7.6	2	1.6	1.7	6.1	3.7	13.1
	Living trees	4.1	8.5	2	2.3	3.5	7.5	6.4	13.2
	Snags	4.8	5.3	1.5	0.1	0.4	0.5	6.8	14.3
	Cavity	5.3	6	1.9	1.8	3.9	5.8	7.8	13.2
	Conk	5.4	9.9	0.9	2	3.5	6.3	9	17.6
	Crack	5	7.9	2	1.7	1.9	4.8	5.3	11.4
Diversity	Total	**0**	1.7	2	2.2	**0**	1.6	**0**	**0**
	Living trees	0.6	4.4	2.1	2	1.7	5.3	1	2.9
	Snags	4.7	3	1.1	**0**	0.6	**0**	7.3	14.1
Management abandonment		1.3	**0**	0.5	1.9	3	8.1	3.3	8.8
Basal area of large living trees		3.9	7.4	2	1.5	2.8	7	5.3	12.2
Large snag volume		2	0.4	1.2	1.7	3.1	4	7.5	15.2
Large log volume		3.7	4.8	2.1	1.4	3.6	8.1	6.4	13.6

3. Saproxylic beetles

		Total		Rare species		Shade-tolerant species		Cavity dwellers		Fungi dwellers	
Explanatory variables		SR	Ab	SR	Ab	SR	Ab	SR	Ab	SR	Ab
	Null model	2.7	4.3	**0**	1.4	1.3	2	0.6	0.1	0.7	4.5
Density	Total	0.9	3.9	1.6	2.3	3.4	4	2	1.6	2.8	4.5
	Trees w/ ≥ 3 types	1.9	5	1.7	2.9	3.4	4	**0**	0.1	2.5	4.1
	Living trees	3	3.3	2	3.4	3.4	4.1	1.9	1.4	2.8	6
	Snags	**0**	6.4	0.7	**0**	3	3.8	2.7	2.1	2.8	2.2
	Cavity	4.7	5.8	1.8	3.2	3.2	4.1	0.4	**0**	1.2	**0**
	Conk	1.3	5.8	0.3	0.5	**0**	0.4	2.3	1.8	2.1	6.6
	Crack	0.1	2.8	1.8	2.9	3.4	3.9	2.3	1.5	1.7	5.6
Diversity	Total	4.6	6.2	2.1	3.4	3.4	2.1	1.9	1.3	2.6	6.4
	Living trees	4.7	6.3	2	3.4	3.4	2.8	2.2	1.6	2.4	6.4
	Snags	0.7	6.3	1.7	1.8	3.2	1.8	2.3	1.8	2.8	1.8
Management abandonment		0.9	1.5	1.8	2.5	1.8	2.8	1	0.3	2.6	6.6
Basal area of large living trees		3.6	2.1	1.7	2.5	3.4	1	2.7	2.1	**0**	4.5
Large snag volume		4.7	3.4	1.9	3.5	3.3	**0**	2	1.4	2.8	6.6
Large log volume		3.7	**0**	0.1	2.8	2.8	1.3	2.4	1.9	2.8	6.2

*Annexe 16 : Standardized estimated coefficients issued from structural equation models for community level analyses. Lines in bold concern the main response variable (i.e. richness or abundance, Poisson error distribution and log-link). The other variables have Gaussian error distributions with an identity link. Lines in italics and variables preceded by "~~" have correlated errors in the models. UNM: unmanaged stands; SE: standard errors of the mean; ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result. NA: not available.*

1. Bat richness

Response variable	Predictor	Estimate	SE	p	
Total richness	**Microhabitat diversity**	**0.173**	**0.074**	**0.019**	*****
Microhabitat diversity	Basal area of large living trees	0.691	0.053	<0.001	***
	Large snag volume	0.135	0.047	0.005	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Forest specialists	**Microhabitat diversity**	**0.209**	**0.113**	**0.064**	**(*)**
Microhabitat diversity	Basal area of large living trees	0.691	0.053	<0.001	***
	Large snag volume	0.135	0.047	0.005	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Cavity roosters	**Microhabitat density (snags)**	**0.353**	**0.137**	**0.010**	*****
Microhabitat density (snags)	Basal area of large living trees	0.172	0.075	0.023	*
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat density (snags)	*~~ Large snag volume*	*0.472*	*NA*	*<0.001*	***

2. Bird richness

Response variable	Predictor	Estimate	SE	p	
Total richness	**Microhabitat diversity**	**0.063**	**0.026**	**0.014**	*****
Microhabitat diversity	Basal area of large living trees	0.691	0.053	<0.001	***
	Large snag volume	0.135	0.047	0.005	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Forest specialists	**Microhabitat diversity**	**0.081**	**0.041**	**0.048**	*****
Microhabitat diversity	Basal area of large living trees	0.691	0.053	<0.001	***
	Large snag volume	0.135	0.047	0.005	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Cavity nesters	**Microhabitat diversity**	**0.134**	**0.044**	**0.002**	******
Microhabitat diversity	Basal area of large living trees	0.691	0.053	<0.001	***
	Large snag volume	0.135	0.047	0.005	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***

3. Saproxylic beetles richness

Response variable	Predictor	Estimate	SE	p	
Total richness	**Management: UNM**	**-0.087**	**0.044**	**0.047**	*****
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Shade tolerant species	**Conk density**	**0.078**	**0.041**	**0.058**	**(*)**
Conk density	Large snag volume	0.108	0.071	0.130	ns
	Basal area of large living trees	0.107	0.077	0.169	ns
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Cavity dwellers	**Density (trees w/ ≥ 3 microhabitat types)**	**0.334**	**0.192**	**0.081**	**(*)**
Density (trees w/ ≥ 3 microhabitat types)	Basal area of large living trees	0.252	0.075	0.001	***
	Large snag volume	0.119	0.065	0.070	(*)
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***

4. Bat abundance

Response variable	Predictor	Estimate	SE	p	
Total abundance	**Microhabitat diversity (snags)**	**0.415**	**0.211**	**0.049**	*
Microhabitat diversity (snags)	Basal area of large living trees	0.228	0.074	0.002	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat diversity (snags)	*~~ Large snag volume*	*0.551*	*NA*	*<0.001*	***
Red-listed species	**Microhabitat diversity (snags)**	**0.716**	**0.303**	**0.018**	*
Microhabitat diversity (snags)	Basal area of large living trees	0.228	0.074	0.002	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat diversity (snags)	*~~ Large snag volume*	*0.551*	*NA*	*<0.001*	***
Forest specialists	**Microhabitat diversity (snags)**	**0.613**	**0.260**	**0.019**	*
Microhabitat diversity (snags)	Basal area of large living trees	0.228	0.074	0.002	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat diversity (snags)	*~~ Large snag volume*	*0.551*	*NA*	*<0.001*	***
Cavity roosters	**Management: UNM**	**1.064**	**0.301**	**<0.001**	***
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***

5. Bird abundance

Response variable	Predictor	Estimate	SE	p	
Total abundance	**Management: UNM**	**0.107**	**0.033**	**0.001**	****
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Red-listed species	**Microhabitat diversity (snags)**	**0.108**	**0.069**	**0.118**	**ns**
Microhabitat diversity (snags)	Basal area of large living trees	0.228	0.074	0.002	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat diversity (snags)	*~~ Large snag volume*	*0.551*	*NA*	*<0.001*	***
Forest specialists	**Microhabitat diversity (snags)**	**0.100**	**0.034**	**0.003**	****
Microhabitat diversity (snags)	Basal area of large living trees	0.228	0.074	0.002	**
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat diversity (snags)	*~~ Large snag volume*	*0.551*	*NA*	*<0.001*	***
Cavity nesters	**Management: UNM**	**0.204**	**0.064**	**0.001**	****
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***

6. Saproxylic beetle abundance

Response variable	Predictor	Estimate	SE	p	
Total abundance	**Basal area of large living trees**	**-0.126**	**0.060**	**0.037**	*****
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Rare species	**Microhabitat density (snags)**	**0.184**	**0.097**	**0.058**	**(*)**
Microhabitat density (snags)	Basal area of large living trees	0.172	0.075	0.023	*
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
~~ Microhabitat density (snags)	*~~ Large snag volume*	*0.472*	*NA*	*<0.001*	***
Shade tolerant species	**Large snag volume**	**-0.131**	**0.063**	**0.040**	*****
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Cavity dwellers	**Cavity density**	**0.276**	**0.196**	**0.158**	**ns**
Cavity density	Large snag volume	0.235	0.066	<0.001	***
	Basal area of large living trees	0.175	0.073	0.018	*
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***
Fungus dwellers	**Cavity density**	**0.190**	**0.072**	**0.008**	******
Cavity density	Large snag volume	0.235	0.066	<0.001	***
	Basal area of large living trees	0.175	0.073	0.018	*
Basal area of large living trees	Management: UNM	0.275	0.108	0.011	*
Large snag volume	Management: UNM	0.588	0.125	<0.001	***
Large log volume	Management: UNM	0.570	0.122	<0.001	***
~~ Large snag volume	*~~ Basal area of large living trees*	*0.251*	*NA*	*<0.001*	***
~~ Large log volume	*~~ Large snag volume*	*0.376*	*NA*	*<0.001*	***

Annexes E : Profiles of tree-related microhabitats in European primary beech-dominated forests – For. Ecol. Man. 489: 363-374 (2018)

**Daniel Kozák[1*], **Martin Mikoláš[1,2], Marek Svitok[3,4], Radek Bače[1], Yoan Paillet[5], Laurent Larrieu[6], Thomas A. Nagel[1,7], Krešimir Begovič[1], Vojtěch Čada[1], Abdulla Diku[8], Michal Frankovič[1], Pavel Janda[1], Ondrej Kameniar[1], Srđan Keren[9], Peter Kjučukov[1], Jana Lábusová[1], Thomas Langbehn[1], Jakub Málek[1], Stjepan Mikac[10], Robert C. Morrissey[1], Markéta Nováková[1], Jonathan S. Schurrman[1], Kristýna Svobodová[1], Michal Synek[1], Marius Teodosiu[11,12], Elvin Toromani[13], Volodymyr Trotsiuk[1,14,15,16], Lucie Vítková[1] Miroslav Svoboda[1]

[1] *Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, Praha 6 – Suchdol 16521, Czech Republic*
[2] *PRALES, Odtrnovie 563, 013 22 Rosina, Slovakia*
[3] *Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, Masaryka 24, 96053 Zvolen, Slovakia*
[4] *Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760, 37005 České Budějovice, Czech Republic*
[5] *Irstea, UR EFNO, Domaine des Barres, 45290 Nogent-sur-Vernisson, France*
[6] *INRA, UMR1201 DYNAFOR, Chemin de Borde Rouge, Auzeville, CS 52627, 31326 Castanet Tolosan Cedex, France; laurent.larrieu@inra.fr; and CRPFOcc, 7 chemin de la Lacade, 31320 Auzeville Tolosane, France*
[7] *Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, 1000 Ljubljana, Slovenia*
[8] *PSEDA-ILIRIA organization, Tirana 1000, Albania*
[9] *Department of Biometry and Forest Productivity, Faculty of Forestry, University of Agriculture in Krakow, al. 29-Listopada 46, 31-425 Krakow, Poland*
[10] *University of Zagreb, Forestry Faculty, Department of Forest Ecology and Silviculture, Svetošimunska 25, 10002, Zagreb, Croatia*
[11] *"Marin Drăcea" National Research-Development Institute in Forestry, Station Câmpulung Moldovenesc, Calea Bucovinei 73b, 725100 Câmpulung Moldovenesc, Suceava, Romania*
[12] *Ștefan cel Mare University of Suceava, Universității 13, 720229 Suceava, Romania*
[13] *Agricultural University of Tirana, Faculty of Forestry Sciences, 1029 Koder-Kamez, Albania*
[14] *Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland*
[15] *SwissForestLab, CH-8903 Birmensdorf, Switzerland*
[16] *Institute of Agricultural Sciences, ETH Zurich, CH-8092 Zurich, Switzerland*
*Corresponding author at: Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129, Praha 6 – Suchdol 16521, Czech Republic. E-mail address: kozakd@fld.czu.cz (D. Kozák). **These authors contributed equally to the work

Abstract

Tree-related microhabitats (TreMs) are important features for the conservation of biodiversity in forest ecosystems. Although other structural indicators of forest biodiversity have been extensively studied in recent decades, TreMs have often been overlooked, either due to the absence of a consensual definition or a lack of knowledge. Despite the increased number of TreM studies in the last decade, the role of drivers of TreM profile in primary forests and across different geographical regions is still unknown. To evaluate the main drivers of TreM density and diversity, we conducted the first large-scale study of TreMs across European primary forests. We established 146 plots in eight primary forests dominated by European beech (Fagus sylvatica L.) in the Carpathian and Dinaric mountain ranges. Generalized linear mixed effect models were used to test the effect of local plot characteristics and spatial variability on the density and diversity (alpha, beta, and gamma) of TreMs. Total TreM density and diversity were significantly positively related with tree species richness and the proportion of snags. Root mean square tree diameters were significantly related to alpha and gamma diversity of TreMs. Both regions reached similarly high values of total TreM densities and total TreM densities and diversity were not significantly different between the two regions; however, we observed between the two regions significant differences in the densities of two TreM groups, conks of fungi and epiphytes. The density and diversity of TreMs were very high in beech-dominated mountain primary forests, but their occurrence and diversity was highly variable within the landscapes over relatively short spatial gradients (plot and stand levels). Understanding these profile provides a benchmark for further comparisons, such as with young forest reserves, or for improving forest management practices that promote biodiversity.

Keywords: Biodiversity indicators, Old-growth, Mountain beech forest, TreMs, Snags, Habitat tree

Introduction

The natural development and the varied timing and intensity of disturbances within primary forests often results in high levels of structural heterogeneity (Bauhus et al., 2009). Certain structural elements, such as high volumes of accumulated standing and lying deadwood (Nagel et al., 2017a), large canopy (veteran) trees (Commarmot et al., 2013), and a diverse array of tree-related microhabitats (TreMs; Larrieu et al., 2018), are often abundant in primary forests. These structural elements are important features for the maintenance and conservation of biodiversity (Lindenmayer et al., 2006), and they are widely recognized as an important feature of conservation management plans (Kraus and Krumm, 2013). Although structural indicators of forest biodiversity have been a major research topic in recent decades, TreMs have often been overlooked, either due to the absence of a consensual definition or a lack of knowledge (Paillet et al., 2017). Larrieu et al. (2018) defined TreMs as a distinct, well-delineated structure occurring on living or standing dead trees that constitute a particular and essential substrate or life site for species or communities to develop, feed, shelter, or breed during at least a part of their life cycle. They are specific aboveground tree morphological singularities that are not found on every tree. The origins of TreMs encompass both endogenous modifications, caused by biotic and abiotic factors, such as intrusions, lesions, and breakages that expose sap and heartwood and initialize outgrowth structures and wood decay (saproxylic TreM), as well as exogenous elements that are physically linked to the tree (epixylic TreM).

Many recent TreM studies have largely been conducted in managed forests or forest reserves historically influenced by harvesting (e.g. , Paillet et al., 2017; Regnery et al., 2013a; Vuidot et al., 2011), and studies have been largely restricted to a few distinct forest types in the Mediterranean, Western Europe, and the USA (Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Regnery et al., 2013b; Winter et al., 2015). Forest management often encourages the production of uniform stands through the logging of high value trees and the removal of damaged or large trees with limited economic value. Conventional forest management systems sometimes create TreMs, such as dendrothelms or bark loss, due to damage during harvesting operations (Larrieu et al., 2012; Vuidot et al., 2011). However, most of the TreM types are typically removed or never develop (Paillet et al., 2017). It is widely documented that TreMs are more abundant and diverse in unmanaged stands (e.g. , Paillet et al., 2017; Winter and Moller, 2008; Winter et al., 2015). The negative effects of forest management on the occurrence of TreMs can largely be explained by the lack of structural features and differences in tree species composition (Keren et al., 2017). Many of these structural components, such as snags and large trees, are considered to be important drivers of TreM diversity and abundance (Keren and Diaci, 2018; Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Vuidot et al., 2011). Only a few studies have been conducted in forests that have developed naturally for at least a century (Larrieu et al., 2014a,b; Courbaud et al., 2017). Primary forests may serve as suitable reference points compared to forests with former management because they tend to have more complex structure and are thus more favorable for many forest-dwelling species (Hunter, 1999; Peterken, 1996).

The importance of studies carried out in primary forests has increasingly been recognized (Commarmot et al. 2013), however, the temperate forests of Europe have a complex land use history, as they have been used for a variety of purposes, such as for fuel wood, pasture, and timber extraction, since ancient times (Sabatini et al., 2018; Veen et al., 2010). Despite extensive forest exploitation in the middle ages and intensive commercial forest management more recently, large patches of primary forests were spared in some remote mountainous areas of central, eastern, and southeastern European countries (Veen et al., 2010). Within Europe, the southeastern European mountain ranges (Carpathians, Dinarides) contain some of the largest areas of well-preserved primary forests, primarily in old-growth stages of development, dominated by European beech (*Fagus sylvatica* L.)(Meyer et al., 2003; Standovár and Kenderes, 2003). There are currently few censuses of TreMs from primary forests because these forests are rare in Europe and they are usually located in remote mountain regions (Parviainen, 2005; Sabatini et al., 2018).

Despite the increased number of TreM studies in the last decade, the role of drivers of TreM densities and diversity is still unknown at the plot and stand scales across different geographical regions (Paillet et al., 2017). Differences in precipitation, temperature, topography, soils, and bedrock play an important role in the development of forest structure, and TreMs develop at differing rates (Paillet et al., 2017). Natural disturbance regimes are another important driver of stand structure in primary forests (Schurman et al., 2018), and studying remnants of primary forests may help us understand the spatial distribution of TreMs under natural conditions (Larrieu et al. 2018). External biotic factors, such as population dynamics of woodpeckers that create cavities, may also influence the production of certain TreMs (Remm and Lõhmus 2011).

This study examines TreM profile from temperate primary forests dominated by European beech in two distinct mountainous regions – the Carpathians and Dinarides. Our objectives were: (i) to provide reference values of TreM density and diversity measures in mountainous mixed beech primary forests and (ii) to evaluate the importance of local plot structure and spatial variability for TreM density and diversity.

Material and methods

Study area and site selection

We refer to "primary forest" as a forest without signs of direct human impact (Figure 1, Table 1), and where natural disturbances are the primary driver of forest structure and composition. These forests not only include old growth, but also the early seral stages of development. Potential study forests were selected using previous inventories of primary forest remnants when available (e.g. , Veen et al., 2010), searching the available archival information, and historical data regarding the land use history of these areas. Almost all study forests are parts of formally protected areas (*i.e.*, national parks, natural parks, strict forest reserves, UNESCO World Heritage sites), or they are proposed to soon be part of protected areas (*i.e.*, Curai i Eperm, Ramino Korito). During the initial field surveys, all forests were inspected for various indicators of naturalness (e.g. , coarse woody debris in various stages of decay, pit-and-mound topography, large trees, natural tree species composition) and signs of human impact; forests with evidence of past logging and grazing and those in close proximity (ca. 500 m) to formerly grazed areas were avoided. Preliminary dendrochronological analysis of selectively chosen tree cores from the study stands (30-40 trees per stand) revealed that a significant number of trees in each stand were older than 350 years, and one tree was even more than 450 years old (located at Perućica).

We selected four primary European beech-dominated mountain forests from both regions. Stands from the Carpathian Mountains spanned Slovakia and Romania, and those from the Dinarides were located in Croatia, Bosnia and Herzegovina, and Albania. The dominant tree species in these forests was European beech, mixed with mainly silver fir (*Abies alba* Mill.), maples (*Acer* spp. L.), and ashes (*Fraxinus* spp. L.).

In the Carpathians, the Slovakia Havešová (HAV) study site was located in the Bukovské Mountains. Havešová lies within Poloniny National Park and it is part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany. In Romania, the selected study forests, Bistra Valley (BIS), Crivia (CRI), and Paulic (PAU), were located in the Maramures Mountains, which are formally protected within Maramures Natural Park, located on the Romanian-Ukrainian border.

In the Dinarides, the Ramino Korito (RAM) study site is situated in Velebit Nature Park in the Velebit Mountains of Croatia. The Curraj i Eperm (CUR) and Lumi i Gashit (LUM) sites are part of Nikaj-Mërtur Regional Nature Park located in the Albanian Alps. Lumi i Gashit (Gashi River) is also part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and Other Regions of Europe. The site in

Bosnia and Herzegovina was located in the Perućica primary forest (PER), which is part of Sutjeska National Park.

There are broad environmental differences between our study sites of the Eastern Carpathians and the Dinarides that are important to point out (Table 1). The average annual precipitation and temperature are higher in the Dinaric region compared to the Carpathian sites. Bedrock in the Dinaric sites is primarily limestone, while in the Carpathians sites it is primarily flysch and gneiss. The sites in the Carpathians were also located on steeper slopes.

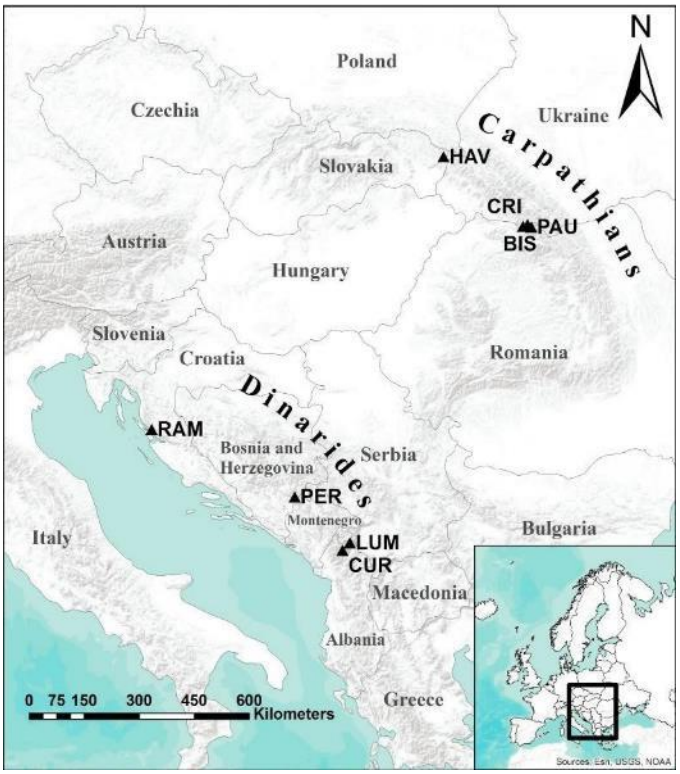


***Figure 1**. Locations of primary forest study areas in the Carpathians and Dinarides*

Table 1: *Study stand characteristics from the Dinaric (CUR, LUM, PER, RAM) and Carpathian (CRI, HAV, BIS, PAU) mountain ranges. Climate characteristics were obtained using the KNMI Climate Explorer (Oldenborgh et al., 2009). Mean temperature and mean annual precipitation were calculated using measurements from 1901 to 2016.*

Country	Forest	Number of plots	Elevation range (m a.s.l.)	Mean annual precipitation (mm)	Mean temperature range (°C)	Average slope (°)	DBH mean (DBH max) (cm)	Broadleaved-Coniferous ratio (%)	Snags (% from all trees)	Mean number of trees per ha (DBH > 6 cm)	Mean number of TreM-bearing trees per ha
	Dinarides										
Albania	Curraj i Eperm (CUR)	14	1019-1287	1237	7.1-8.4	19.6	24.9 (124.1)	99:1	13	878	306.7
Albania	Lumi i Gashit (LUM)	14	1223-1682	1162	5.9-7.9	27.4	26.1 (135)	58:42	8	820	247.6
Bosnia	Perućica (PER)	48	1057-1450	1157	5-7.2	24.7	24.4 (134.5)	60:40	12	951	321.4
Croatia	Ramino Korito (RAM)	16	820-984	1299	8.1-8.9	15.4	32.1 (97.9)	91:9	16	518	281.6
	Carpathians										
Romania	Crivia (CRI)	14	874-1147	862	4.2-5.6	34.7	28.1 (120)	77:23	7	533	311.4
Romania	Paulic (PAU)	12	942-1097	830	4.4-5.2	33.7	32.2 (163)	76:24	17	559	350.6
Romania	Bistra (BIS)	14	959-1154	830	4.1-5.1	35.4	32.2 (107.6)	69:31	9	477	176.7
Slovakia	Havešová (HAV)	14	615-710	815	6-6.5	23.4	25.5 (130)	100:0	13	572	226.7

Stand structural data

For the selection of permanent study plots, a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each 10-ha polygon we generated a random point to establish sampling points where we established two plots. The paired plots consisted of two 1,500 m2 circular plots (radius of 21.85 m); each plot center was located 40 m in opposite directions from the random sample point and parallel to the slope contour (Appendix 1). We established 146 permanent research plots nested within 73 pairs of plots across 8 forest stands. For each tree with diameter at breast height (DBH) ≥ 6 cm, the status of all trees (live or snag), tree species, and TreM presence/absence were recorded.

TreM data

For all study plots, each tree, including the stem and crown, was visually inspected for TreMs by two observers. Based on the typology of Vuidot et al. (2011), we created a list of 30 TreM types that we used to classify TreMs on our plots. All living trees with a DBH > 6 cm and snags located within the plots were searched for presence of TreMs (Appendix 2); we surveyed 13,640 living trees and snags in total. We arranged the TreM types into 12 groups for further analysis according to Paillet et al. (2017): crown deadwood, broken tops, conks of fungi, woodpecker cavities, non-woodpecker cavities, base cavities, bark characteristics, cracks, outgrowths, patches with exudates, epiphytes, and dendrothelms. All TreMs were surveyed in 2015 and 2016 during the period of June to September.

TreM characteristics

Diversity and density measures of TreMs were quantified for each sample plot. To reflect the diversity of TreM types, diversity was defined in terms of the number of TreM types occurring within the plot. Alpha diversity was defined as the average number of TreM types per tree in a given plot. Because the number of trees varied widely among plots (27–277 trees per plot), gamma diversity was calculated as the total number of TreM types per plot standardized by rarefaction to a common abundance level (n = 27 trees) to ensure comparability across plots (Chao et al., 2014). Beta diversity was defined as the ratio of gamma to alpha diversity, as originally proposed by Whittaker (1960); this ratio measures the degree to which TreM composition changes from tree to tree within a given plot.

To identify TreM densities, we used the index proposed by Paillet et al. (2017), *i.e.* the density of TreM-bearing trees, which allowed us to compare our results with other studies that used the same indices. Density of TreMs was quantified as the sum of TreM-bearing trees extrapolated to one hectare (Paillet et al., 2017). To determine the number of trees per plot bearing a given TreM type, each TreM type found on a tree was counted only once, even if it was present in greater numbers. Diversity and density measures were also calculated for several broad groups of TreM types (Table 2), in which case when we refer to density, it defines the density of trees bearing a particular TreM type. A major advantage of this sampling design was the minimal amount of time an observer needed to access TreMs in the field. Although we did not record the true abundance of all TreM types, our approach allowed us to compare our TreM data with other studies that used the same method (e.g. , Paillet et al., 2017; Vuidot et al. 2011).

Data analyses

Generalized linear mixed models (GLMMs) were used to assess the effect of local plot structure and spatial variability on diversity and density characteristics of TreMs. Fixed effects included tree species richness (*i.e.*, total number of tree species per plot), RMS DBH (root mean square diameter of trees at

breast height in a given plot), proportion of snags (proportion of snags per plot versus total number of trees), and region (Dinarides and Carpathians). The random effects structure mirrored the spatial hierarchical nature of the sampling design, including plots nested within pairs of plots, which were nested within stands nested within regions. In the models of TreM density, the tree density per plot was treated as a nuisance variable to account for a trivial positive relationship between tree density and TreM density. Because diversity and density of TreMs are strictly positive and continuous variables, we used GLMMs with a gamma error distribution and log link function (McCullagh and Nelder, 1989). Model parameters were estimated using Laplace approximation and their significance was tested using likelihood ratio tests (Bolker et al., 2009). There was no serious multicollinearity observed in the models (all VIFs < 2.3). To compare the relative importance of the fixed effects, we calculated semi-partial marginal determination coefficients (R^2_m; Nakagawa et al., 2017) derived from a commonality analysis (Ray-Mukherjee et al., 2014). The intraclass correlation coefficients (ICC) were used to quantify the proportion of variance explained by each of the hierarchical spatial levels. All analyses were performed in R language version 3.4.3 (R Core Team, 2017) using the lme4 library (Bates et al., 2015).

Results

Total TreM densities

Total mean density of TreM-bearing trees (number of trees bearing at least one TreM) was similar in the Carpathians (266.4 bearing-trees ha^{-1}) and Dinarides (289.3 bearing-trees ha^{-1}). The average density of TreM-bearing trees for all stands was 277.8 TreM-bearing trees ha^{-1}. Epiphytes (128.8 bearing-trees ha^{-1}), bark characteristics (101.2 bearing-trees ha^{-1}), base cavities (65.2 bearing-trees ha^{-1}), and non-woodpecker cavities (41.3 bearing-trees ha^{-1}) had the highest TreM densities in both regions (Table 2). The lowest densities were observed for outgrowths (9.9 bearing-trees ha^{-1}) and dendrothelms (4.6 bearing-trees ha^{-1}). In the Carpathians, bark characteristics (112.7 bearing-trees ha^{-1}) and base cavities (98.9 bearing-trees ha^{-1}) had the highest densities, and dendrothelms (1.6 bearing-trees ha^{-1}) had the lowest density. The Dinarides were characterized by high TreM densities of epiphytes (168.7 bearing-trees ha^{-1}) and non-woodpecker cavities (48.7 bearing-trees ha^{-1}), and low densities of patches with exudates (8.6 bearing-trees ha^{-1}), outgrowths (7 bearing-trees ha^{-1}), and broken tops (10.1 bearing-trees ha^{-1}).

Key factors to the diversity of TreMs

Tree species richness, RMS DBH, and the proportion of snags showed significant relationships to TreM alpha diversity (*i.e.*, the mean number of TreM types per tree), and gamma diversity (*i.e.*, the total number of TreM types per plot; Table 3). All these habitat properties were positively correlated with the TreM diversity measures (Figure 2). RMS DBH displayed a relatively strong relationship with TreM alpha (R^2_m = 12.2%) and gamma diversity (R^2_m = 13.2%), but the effect of tree diversity was rather negligible ($R^2_m \leq$ 0.6%). In contrast, beta diversity, the TreM turnover among trees, was unaffected by tree DBH. Considering spatial variability, alpha, beta, and gamma diversity of TreMs varied widely within paired plots (ICC > 35%) and also among pairs within stands (ICC ~ 23–25%). The contribution of stands to the observed variation was less obvious, but still important (ICC ~ 9–14%), with the exception of beta diversity, where the between-stand component of variance was not significant. We did not find any significant differences in TreM diversity between the Carpathians and Dinarides.

Key factors to the density of TreMs

Total density of TreMs was significantly and positively correlated with tree species richness and the proportion of snags in plots; RMS DBH showed no significant relationship with total TreM density

(Figure 2). Total TreM density significantly varied among plots, pairs of plots, and stands, but there was no significant difference in overall TreM density between regions (Table 3).

The density of broken tops, patches with exudates, and epiphytes displayed a significant and positive relationship with tree species richness. RMS DBH was positively related with density of conks of fungi, base cavities, epiphytes, and outgrowths, and it was negatively related with crown deadwood and density of broken tops. The density of most TreMs was significantly correlated with the proportion of snags, both positively (crown deadwood, conks of fungi, woodpecker, bark characteristics, patches with exudates) and negatively (outgrowth). Significant differences between regions were observed for the density of conks of fungi and epiphytes; the first group showed higher densities in the Carpathians, while the latter group was higher in Dinarides. There was also a higher density of outgrowths and broken tops in the Carpathians, although the relationships were marginally non-significant (Table 3). These large-scale geographic trends were accompanied by high similarity of TreM densities among stands within regions (non-significant stand effects). In contrast, densities of the other TreM groups varied considerably at smaller spatial scales (plots, pairs of plots, stands), and consistent large-scale differences between regions were not evident.

Table 2: *Tree-related microhabitat densities for different TreM groups for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All densities are presented as* ha^{-1} *values.*

TreM group	Total TreM density	Carpathians	Dinarides	Snags total	Snags Carpathians	Snags Dinarides	Living trees total	Living trees Carpathians	Living trees Dinarides
Crown deadwood	33.1	31.6	33.9	1.5	2.8	0.7	31.6	28.8	33.3
Broken tops	17.3	29.6	10.1	3.8	6.9	2.0	13.5	22.7	8.1
Conks of fungi	21.8	33.1	15.2	17.7	26.4	12.6	4.1	6.7	2.6
Woodpecker cavities	13.3	15.9	11.7	11.1	12.5	10.3	2.2	3.5	1.4
Non-woodpecker cavities	41.3	28.8	48.7	10.2	7.2	12.0	31.1	21.6	36.7
Base cavities	65.7	98.9	46.2	8.0	10.5	6.5	57.7	88.4	39.7
Bark characteristics	101.2	112.7	94.4	59.1	53.6	62.3	42.1	59.1	32.1
Cracks	30.3	23.7	34.2	7.9	10.4	6.4	22.5	13.3	27.8
Outgrowth	9.9	14.8	7.0	0.8	0.7	0.8	9.1	14.1	6.2
Patches with exudates	16.0	28.5	8.6	1.1	1.5	0.9	14.8	27.0	7.7
Epiphytes	128.8	60.7	168.7	15.8	11.5	18.3	113.0	49.3	150.4
Dendrothelms	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
SUM	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

Table 3: *Summary of GLMMs relating diversity (alpha, beta, gamma) and density of microhabitats to fixed and random effects. Likelihood ratio test statistics (χ^2), probabilities (p), semi-partial marginal determination coefficients (R^2_m [%]), and intra-class correlation coefficients (ICC [%]) are displayed. Significant positive/negative partial relationships (r) are designated by +/- signs, respectively; inequality signs are used for comparisons between Carpathians (C) and Dinarides (D). Model parameters were considered significant at 5% and are highlighted in bold.*

	Fixed effects															Random effects								
	Tree species richness				RMS DBH				Proportion of snags				Region				Stand			Paired plots			Plot		
Model	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	ICC	χ^2	p	ICC	χ^2	p	ICC
Alpha diversity	**6.3**	**0.0121**	**0.6**	**+**	**64.3**	**< 0.0001**	**12.2**	**+**	**41.8**	**< 0.0001**	**7.2**	**+**	0.3	0.6152	1.4		**8.6**	**0.0034**	**9.4**	**84.3**	**< 0.0001**	**23.0**	**107.9**	**< 0.0001**	**48.0**
Beta diversity	**9.9**	**0.0016**	**2.2**	**+**	1.5	0.2223	< 0.1		**12.4**	**0.0004**	**4.6**	**+**	2.8	0.0962	9.0		2.2	0.1395	11.7	**64.3**	**< 0.0001**	**24.3**	**74.5**	**< 0.0001**	**42.1**
Gamma diversity	**10.5**	**0.0012**	**0.2**	**+**	**52.9**	**< 0.0001**	**13.2**	**+**	**16.5**	**0.0001**	**2.6**	**+**	1.0	0.3176	5.5		**11.8**	**0.0006**	**13.6**	**62.9**	**< 0.0001**	**25.2**	**63.5**	**< 0.0001**	**36.5**
Density																									
All microhabitats	**10.6**	**0.0011**	**7.3**	**+**	< 0.1	0.8353	< 0.1		**29.7**	**< 0.0001**	**14.4**	**+**	0.1	0.7811	< 0.1		**4.7**	**0.0294**	**5.7**	**100.9**	**< 0.0001**	**33.8**	**85.7**	**< 0.0001**	**44.0**
Crown deadwood	0.4	0.5135	0.2		**15.2**	**0.0001**	**7.2**	**-**	**4.4**	**0.0367**	**1.9**	**+**	0.1	0.7995	< 0.1		**8.1**	**0.0044**	**12.0**	3.5	0.0601	18.0	0.0	0.9708	0.0
Broken tops	**4.3**	**0.0376**	**< 0.1**	**+**	**5.6**	**0.0181**	**1.5**	**-**	1.0	0.3063	< 0.1		3.2	0.0727	13.9		**10.3**	**0.0013**	**19.7**	**50.0**	**< 0.0001**	**26.3**	**28.2**	**< 0.0001**	**32.8**
Conks of fungi	0.4	0.5268	< 0.1		**15.3**	**0.0001**	**7.4**	**+**	**11.8**	**0.0006**	**6.1**	**+**	**5.6**	**0.0178**	**13.3**	**C > D**	**5.4**	**0.0203**	**18.3**	**10.5**	**0.0012**	**12.6**	**15.6**	**0.0001**	**41.1**
Woodpecker cavities	0.1	0.7610	0.0		< 0.1	1.0000	< 0.1		**21.5**	**< 0.0001**	**9.9**	**+**	0.1	0.6993	0.8		**8.4**	**0.0038**	**11.7**	**60.6**	**< 0.0001**	**29.5**	**50.1**	**< 0.0001**	**39.4**
Non-woodpecker cavit.	0.6	0.4444	1.4		0.8	0.3672	0.5		3.2	0.0715	2.1		2.2	0.1419	10.5		**6.6**	**0.0103**	**10.3**	**29.7**	**< 0.0001**	**14.8**	**55.7**	**< 0.0001**	**56.2**
Base cavities	0.2	0.6821	0.7		**6.4**	**0.0112**	**4.6**	**+**	3.1	0.0769	4.8		0.8	0.3585	5.7		**18.9**	**< 0.0001**	**18.7**	**14.0**	**0.0002**	**17.3**	2.9	0.0910	40.6
Bark characteristics	0.8	0.3864	0.4		1.3	0.2631	< 0.1		**50.9**	**< 0.0001**	**18.8**	**+**	0.8	0.3583	2.1		**5.4**	**0.0206**	**7.1**	**70.6**	**< 0.0001**	**25.8**	**99.3**	**< 0.0001**	**50.6**
Cracks	2.8	0.0932	3.4		< 0.1	0.8959	< 0.1		1.0	0.3172	0.9		1.5	0.2140	2.4		0.2	0.6855	1.6	**26.0**	**< 0.0001**	**16.0**	**32.2**	**< 0.0001**	**62.6**
Outgrowth	0.1	0.7428	0.7		**7.0**	**0.0082**	**1.6**	**+**	**7.6**	**0.0058**	**1.2**	**-**	3.8	0.0507	8.3		3.7	0.0529	13.6	**20.3**	**< 0.0001**	**22.4**	**12.5**	**0.0004**	**31.3**
Patches with exudates	**10.2**	**0.0014**	**4.3**	**+**	0.3	0.6099	< 0.1		**4.7**	**0.0299**	**1.2**	**+**	1.6	0.2124	8.1		**22.5**	**< 0.0001**	**25.8**	**53.4**	**< 0.0001**	**17.8**	**66.8**	**< 0.0001**	**40.3**
Epiphytes	**11.4**	**0.0007**	**8.9**	**+**	**5.4**	**0.0204**	**0.5**	**+**	0.5	0.4768	0.9		**6.4**	**0.0116**	**13.9**	**C < D**	< 0.1	0.9968	5.6	**51.1**	**< 0.0001**	**37.1**	**19.9**	**< 0.0001**	**27.6**
Dendrothelms	< 0.1	0.9658	< 0.1		2.1	0.1446	1.0		2.5	0.1146	1.2		2.6	0.1098	6.9		1.3	0.2572	10.9	**42.2**	**< 0.0001**	**26.0**	**35.6**	**< 0.0001**	**33.2**

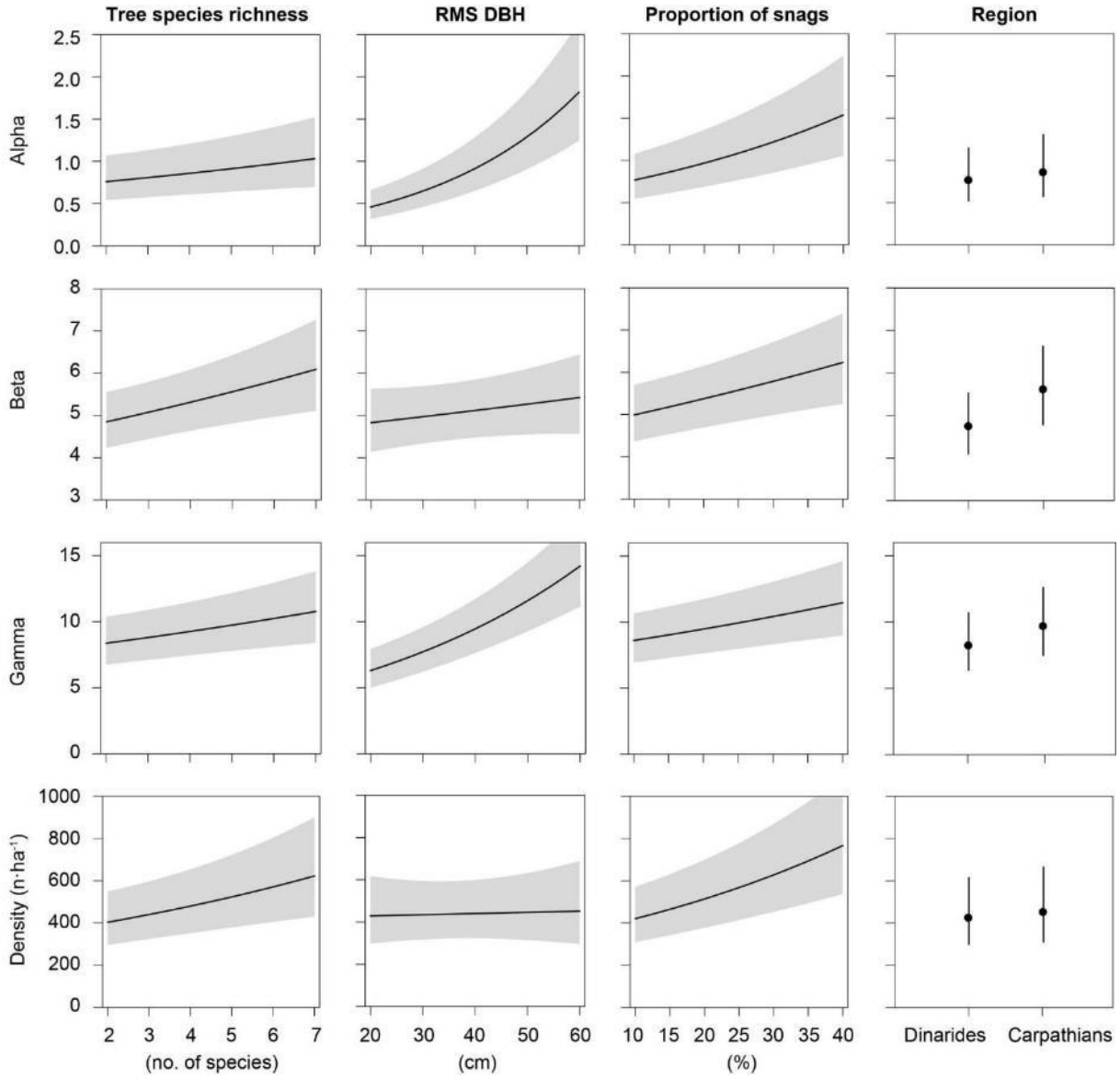


Figure 2. *Effect plots showing the results of GLMMs testing for the effect of tree species richness, RMS DBH, proportion of snags, and region on diversity (alpha, beta and gamma) and density of TreMs. Predicted values (lines, circles) are displayed along with 95% confidence intervals (gray polygons, error bars).*

Discussion

Preserving the diversity of organisms that rely on specific forest structures is a key conservation challenge as forest management intensifies across the globe (Hansen et al., 2013; Mori and Kitagawa, 2014). Our assessment of TreM densities in primary forests provides a valuable benchmark for forest managers and policy makers that seek to implement structures that will benefit a host of species of conservation concern (Vuidot et al., 2011). We performed the first quantitative TreM analyses and comparison of TreM diversity in primary mixed beech-dominated forests in two distinct mountainous regions — the Carpathians and Dinarides. The primary drivers of TreM density (number of trees bearing a particular TreM per hectare) and diversity (richness of TreM types) at the plot scale in these forests were structural characteristics, such as RMS DBH, tree species composition, and proportion of snags. Geographical distance between regions did not play an important role in TreM densities and diversity, either at the alpha, beta, or gamma levels. Our study highlights that TreM densities observed

in the primary forests were significantly higher in comparison to densities presented in studies from managed forests (*e.g.*, Larrieu et al. 2012; Paillet et al., 2017).

We observed a significant increase in total TreMs density and alpha and gamma diversity of TreM types with an increased proportion of snags and tree species richness. Several studies have already observed the importance of snags, large living trees, and different tree species for densities of TreM types (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree diameter has also been recognized as an important factor in TreM dynamics across different forest types; it has been observed to influence the abundance of TreMs (Larrieu and Cabanettes, 2012), the diversity of TreM types (Larrieu et al. 2014a; Vuidot et al., 2011), or the occurrence of some TreM types, such as bark characteristics (Michel and Winter, 2009). Large diameter trees were also important in our study, especially for alpha and gamma diversity of TreMs, and densities of some TreM types. We did not find a significant relationship between DBH and total TreM density; most studies that observed a significant relationship between tree diameter and TreM used the DBH of the individual tree bearing the TreM. In contrast, we used RMS DBH of the trees on a plot, which likely introduced noise into the relationship given the mixed severity disturbance regimes of the region, and we also counted only one TreM type on each TreM-bearing tree, which may also further mask any relationship between diameter and density of TreMs. Tree species composition is another factor that has been observed to influence total TreM density and diversity (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree species diversity has also been observed to positively influence densities of some specific TreMs, such as broken tops, patches with exudates, and epiphytes. Patches with exudates, such as sap-runs and gummosis, are more likely to be found on deciduous trees (Siitonen, 2012), while the excurrent growth habit of conifers makes them more susceptible to broken tops. The proportion of snags had a significant effect on TreM diversity at the alpha, beta, and gamma levels, and also on the overall density of TreMs (Table 3). However, we observed that all TreM types were present within the living trees and snags as well, which may be due to partial mortality, whereby dead wood occurs on living trees, which is characteristic of very large trees (Siitonen, 2012) that could bear TreMs normally present on dead trees in managed forests (e.g. , woodpecker feeding holes). Our findings emphasize the importance of snags in broadleaved stands because they promote increased TreM diversity and densities within beech-dominated primary forests. We also observed higher densities of certain TreM types that are rarer on living trees than on snags (woodpecker cavities, conks of fungi, and bark characteristics), which is consistent with the findings of Vuidot et al. (2011) and Larrieu and Cabanettes (2012) whereby the presence of conks of fungi and woodpecker cavities were significantly higher on snags than on living trees (Appendix 3). Woodpeckers generally prefer to nest and roost in snags, and fungi play an important role in the excavation of woodpecker cavities (Zahner et al. 2012), and woodpeckers are often suggested as a vector for the fungus (Jackson and Jackson, 2004). After the tree dies, the decay process promotes conditions that influence the occurrence of other TreM types, such as bark characteristics and non-woodpecker cavities (Vuidot et al., 2011). Although snags represented only 7-17 % of all trees per stand, they accounted for one-third of the density of all TreMs tallied in our study (Table 2). Our results generally agree with prior TreM research conducted in different regions, and it highlights the positive effects of high levels of structural heterogeneity (e.g. , large trees, and high tree species richness and proportions of snags) to support a diverse array of TreMs. Finally, our results showed higher densities of TreMs associated with certain taxa compared to published conservation guidelines: a minimum of 40 cavities per hectare for the conservation of cavity dwelling birds (Blondel, 2005) or a network of 7 to 10 live cavity- or crack-bearing trees per hectare for bats (Meschede and Heller, 2003). Our data support these findings and demonstrate that the primary forests can reach very high TreM levels.

Here, we compared for the first time TreM densities and diversity between primary forests of the Carpathian and Dinarides mountain ranges. Although precipitation and temperature differ among the regions (Table 1), we did not observe significant differences in total TreM densities or TreM diversity between the regions. Both of the regions had similarly high diversity values (Table 2). However, we

observed significant differences in densities of several TreM types between the regions, including densities of conks of fungi and epiphytes (Table 3), which could potentially be influenced by large-scale climatic differences or soil properties (Ding et al., 2016). However, our results suggested significant variability between TreM densities and diversity on relatively small spatial gradients (stand and plot levels). We observed TreM densities almost two times greater than that of Paillet et al. (2017) in strict mixed mountain forest reserves of France (Table 2; Appendix 2). They determined that strict forest reserves had higher TreM densities, both total and individual densities, than comparable adjacent managed forests. This general trend has also been observed in several other European forests (Winter and Moller, 2008; Winter et al., 2015). Although Paillet et al. (2017) sampled strict forest reserves, the mean time since any previous harvesting was only 48 years; it is impossible to identify the structure of the stands at the beginning of the set-aside period or how intensively the stands were managed prior to their strict reserve designation. We analyzed TreMs exclusively from remote primary forests with very limited access, and it is likely that these stands were never managed; some of the oldest trees are more than 450 years old. Compared to the findings of Paillet et al. (2017), we observed the densities of broken tops was more than 10 times higher on average, and almost 20 times higher in the Carpathians. The higher densities of broken tops may be attributable to the natural disturbance regime that influences structural dynamics in primary forests (Meigs et al., 2017), as well as the high proportion of live trees bearing polypores, such as *Fomes fomentarius* or *Fomitopsis pinicola*, which make beech stems more prone to breakage (Zeibig et al., 2005*)*. In addition, the tree dimensions, taller trees with larger primary branches, may be more prone to partial crown loss. Similar conclusions can be drawn for higher densities of other TreM groups. High volumes and diversity of deadwood, which are typical of primary forests (Nagel et al., 2017a), may influence the presence of conks of fungi and even woodpeckers (Jackson and Jackson, 2004). We also observed much higher densities of base cavities compared to Paillet et al. (2017); because large cavities take more time to develop, higher rates of occurrence on very old trees would be expected, thus many primary forests would have higher numbers of older trees with longer periods of time since the last severe disturbance (Siitonen et al., 2012). In contrast, we found lower densities of outgrowths and bark characteristics in the Dinaric dataset compared to the French strict forest reserves (Paillet et al., 2017); outgrowths and bark characteristics tend to occur more frequently on oaks (*Quercus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.) compared to beech (Vuidot et al., 2011). However, higher densities of outgrowths and bark characteristics were found in the Carpathian dataset than in Dinarides dataset.

Conclusions

We conducted the first assessment of tree-related microhabitats in beech-dominated primary forests of the Carpathian and Dinaric mountain ranges; these sites represent some of the last remnants of primary forests in Europe. Our study provides an empirical analysis of TreM variability and reference values from these primary forests, both of which will help inform forest managers, conservation strategies, and policy decisions. These reference values provide a means to assess the influence of forest management on TreM profile. However, our study sites represent a relatively small fraction of these two vast mountain ranges. To improve our understanding of TreM dynamics, we suggest a more thorough survey of primary forest study areas across the Dinaric and Carpathian Mountains, as well as other mountain ranges where similar forest types occur. Climate characteristics, topographical features, such as the presence of cliffs that can increase the occurrence of certain TreMs, such as bark loss, by rock falls, or biotic factors, such as woodpecker density (or diversity) or the presence of large ungulates, may also play an important role in the availability of TreMs. A potentially important driver of TreM density and diversity may be the natural disturbance regime that may play an important role in creation and maintenance of TreMs. Future research will include the analysis of disturbance history variables in relation to TreMs. In particular, a dendroecological approach could be used to link natural disturbance history with TreM diversity and density, and to assess how forest development influences the distribution of TreMs. Finally, our results show that primary forests maintain high TreM diversity,

and that they may significantly contribute to the overall species diversity across forested landscapes. Although our paper did not directly compare primary forests with managed forests under similar environmental conditions, we also plan to establish plots in managed forests near primary forests in future studies to better understand TreM dynamics and the critical role of protected areas to maintain and enhance biodiversity in our modern world.

Acknowledgement: This project was supported by the institutional project MSMT CZ.02.1.01/0.0/0.0/16_019/0000803, MSMT project LTC17055, through the Czech University of Life Sciences (Grant IGA no. B09/17 and CIGA no. 20184304), by institutional project MSMT EVA4.0 CZ.02.1.01/0.0/0.0/16_019/0000803 and by the European Regional Development Fund-Project "Mechanisms and dynamics of macromolecular complexes: from single molecules to cells" (No. CZ.02.1.01/0.0/0.0/15_003/0000441).

References

Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bauhus, J., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053

Blondel, J., 2005. Bois mort et cavités: leur rôle pour l'avifaune cavicole. Vallauri D, André J, Dodelin B, Eynard-Machet R, Rambaud D, Bois mort et à cavités: une clé pour des forêts vivantes. Lavoisier, Paris, 137-144.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84, 45-67. Stable URL : http://www.jstor.org/stable/43187596

Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V., 2013. Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure.

Courbaud, B., Pupin, C., Letort, A., Cabanettes, A., Larrieu, L., 2017. Modelling the probability of microhabitat formation on trees using cross-sectional data. *Methods Ecol. Evol.*, *8*(10), 1347-1359. https://doi.org/10.1111/ijlh.12426

Ding, Y., Liu, G., Zang, R., Zhang, J., Lu, X., Huang, J., 2016. Distribution of vascular epiphytes along a tropical elevational gradient: Disentangling abiotic and biotic determinants. Sci. Rep. 6. https://doi.org/10.1038/srep19706

ESRI ArcGIS, 2011. "Release 10." *Redlands, CA: Environmental Systems Research Institute* 437.

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science (80-.). 342, 850–853. https://doi.org/10.1126/science.1244693

Hunter, Jr., M.L., 1999. Maintaining biodiversity in Forest Ecosystems. Cambridge Univ. Press. https://doi.org/10.1046/j.1365-2664.1999.00459-3.x

Jackson, J.A., Jackson, B.J.S., 2004. Ecological Relationships Between Fungi and Woodpecker Cavity Sites. Condor 106, 37. https://doi.org/10.1650/7483

Keren, S., Diaci, J., 2018. Comparing the quantity and structure of deadwood in selection managed and old-growth forests in South-East Europe. Forests 9, 1–16. https://doi.org/10.3390/f9020076

Keren, S., Diaci, J., Motta, R., Govedar, Z., 2017. Stand structural complexity of mixed old-growth and adjacent selection forests in the Dinaric Mountains of Bosnia and Herzegovina. For. Ecol. Manage. 400, 531–541. https://doi.org/10.1016/j.foreco.2017.06.009

Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity, European Forest Institute.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Can. J. For. Res. 42, 1433–1445. https://doi.org/10.1139/x2012-077

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014a. Tree microhabitats at the stand scale in montane beech-fir forests: Practical information for taxa conservation in forestry. Eur. J. For. Res. 133, 355–367. https://doi.org/10.1007/s10342-013-0767-1

Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. Eur. J. For. Res. 131, 773–786. https://doi.org/10.1007/s10342-011-0551-z

Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., Deconchat, M., 2014b. Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring. For. Ecol. Manage. 334, 163–173. https://doi.org/10.1016/j.foreco.2014.09.007

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecol. Indic. 84, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. https://doi.org/10.1016/j.biocon.2006.02.019

McCullagh, P., Nelder, J. A., 1989. Generalized Linear Models, 2nd. edition. Chapman and Hall/CRC, USA.

Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., Donato, D.C., Janda, P., Lábusová, J., Seedre, M., Mikoláš, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M., Trotsiuk, V., Vítková, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406, 410–426. https://doi.org/10.1016/j.foreco.2017.07.051

Meschede, A., Heller, K.G. ,2003. Ecologie et protection des chauvessouris en milieu forestier. MHN de Genéve. Le Rhinolophe 16:1–248.

Meyer, P., Tabaku, V., von Lupke, B., 2003. Structural characteristics of Albanian beech (Fagus sylvatica L.) virgin forests - Deductions for semi-natural forestry. Forstwissenschaftliches Cent. 122, 47–58. https://doi.org/10.1046/j.1439-0337.2003.02041.x

Michel, A. K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. For. Ecol. Manage. 257(6), 1453-1464. https://doi.org/10.1016/j.foreco.2008.11.027

Mori, A.S., Kitagawa, R., 2014. Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: A global meta-analysis. Biol. Conserv. 175, 65–73. https://doi.org/10.1016/j.biocon.2014.04.016

Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017a. Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. Biol. Conserv. 216, 101–107. https://doi.org/10.1016/j.biocon.2017.10.008

Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A., Paulic, V., 2017b. The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. For. Ecol. Manage. 388, 29–42. https://doi.org/10.1016/j.foreco.2016.07.047

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14, 20170213. https://doi.org/10.1098/rsif.2017.0213

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manage. 389, 176–186. https://doi.org/10.1016/j.foreco.2016.12.014

Parviainen, J., 2005. Virgin and natural forests in the temperate zone of Europe. For. Snow Landsc. Res. 79, 9–18.

Peterken, G.F., 1996. Natural woodland: ecology and conservation in northern temperate regions, Cambridge University Press.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R., Hamer, M., 2014. Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. Methods Ecol. Evol. 5, 320–328. https://doi.org/10.1111/2041-210X.12166

Regnery, B., Couvet, D., Kubarek, L., Kerbiriou, C., 2013a. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests 34, 221–230. https://doi.org/10.1016/j.ecolind.2013.05.003

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013b. Forest Ecology and Management Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests ? 295, 118–125.

Remm, J., Lõhmus, A., 2011. Tree cavities in forests - The broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manage. 262, 579-85. https://doi.org/10.1016/j.foreco.2011.04.028

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, CH., Lindner, M., Potzchner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. . Where are Europe's last primary forests? Divers. Distrib. 00:1–14. https://doi.org/10.1111/ddi.12778

Schurman, J.S., Trotsiuk, V., Bače, R., Čada, V., Fraver, S., Janda, P., Kulakowski, D., Lábusová, J., Mikoláš, M., Nagel, T.A, Seidl, R., Synek, M., Svobodová, K., Chaskovskyy, O., Teodosiu, M., Svoboda, M., 2018. Large-scale disturbance legacies and the climate sensitivity of primary Picea abies forests. *Global change biology*. https://doi.org/10.1111/gcb.14041

Siitonen, J., 2012. Microhabitats, in: Biodiversity in Dead Wood. pp. 150–182. https://doi.org/10.1017/CBO9781139025843.008

Standovár, T., Kenderes, K., 2003. A review on natural stand dynamics in beechwoods of east central Europe. Appl. Ecol. Environ. Res. 1, 19–46.

Van Oldenborgh, G.J., Drijfhout, S., Van Ulden, A., Haarsma, R., Sterl, A., Severijns, C., Hazeleger, W., Dijkstra, H., 2009. Western Europe is warming much faster than expected. Clim. Past 5, 1–12. https://doi.org/10.5194/cp-5-1-2009

Veen, P., Fanta, J., Raev, I., Biriş, I.A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: Results of two national inventory projects and their implications for protection. Biodivers. Conserv. 19, 1805–1819. https://doi.org/10.1007/s10531-010-9804-2

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144, 441–450. https://doi.org/10.1016/j.biocon.2010.09.030

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. https://doi.org/10.2307/1943563

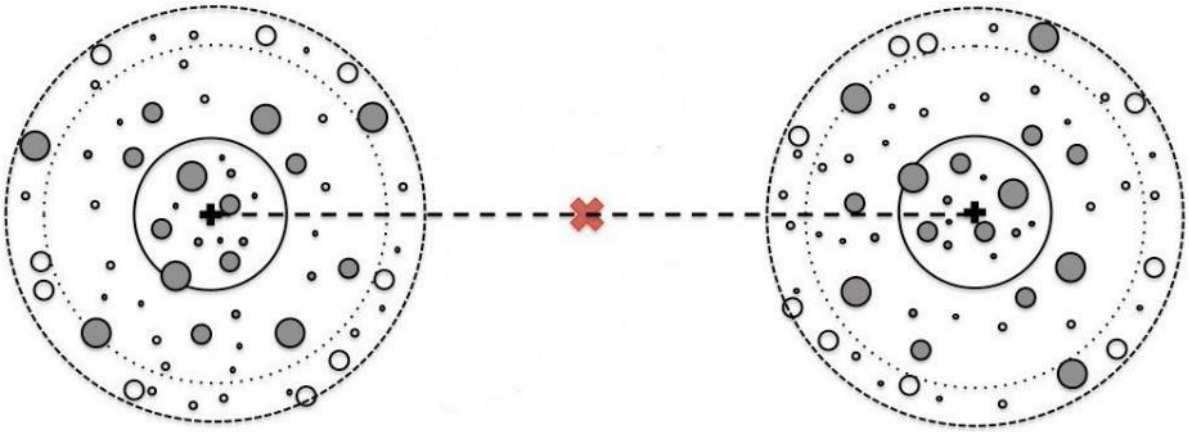
Winter, S., 2015. Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. Eur. J. Forest. Res. 134, 335–347. https://doi.org/10.1007/s10342-014-0855-x

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manage. 255, 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029

Zahner, V., Sikora, L.,Pasinelli, G. 2012. Heart rot as a key factor for cavity tree selection in the black woodpecker. For. Ecol. Manage. 271, 98-103.

Zeibig, A., Diaci, J., Wagner, S. 2005. Gap disturbance patterns of a Fagus sylvatica virgin forest remnant in the mountain vegetation belt of Slovenia. For. Snow Landsc. Res. 79, 69-80.

Appendix 1: *Example of the nested plot structure. The red cross indicates the randomly generated navigation point used to locate the pair of circular sample plots.*



***Appendix 2** : Tree-related microhabitats densities for all surveyed TreM types for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All densities are presented as ha^{-1} values.*

TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Woodpecker cavities	X	Woodpecker cavities with >2cm aperture, woodpecker breeding or feeding holes	289	13.2	15.9	11.6	11.1	12.5	10.2	2.1	3.5	1.4
Non-woodpecker cavities	X(partially)	Non-woodpecker cavities with >5cm aperture anywhere on the trunk: formed after injury, branch fall	744	34.0	22.7	40.6	4.1	2.6	4.9	29.9	20.1	35.7
Non-woodpecker cavities	X	Cavity string: at least three woodpecker cavities in a stem with a maximum distance of two meters between two cavity entrances. Cavity strings are an important starting point for the development of deep and long lasting stem cavities	161	7.4	6.0	8.1	6.1	4.6	7.0	1.2	1.5	1.1
Woodpecker cavities		Shallow cavities in the bark arranged in a ring; usually woodpecker	2	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree without mold	884	40.4	62.3	27.5	2.4	3.6	1.7	38.0	58.8	25.8
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree with mold	525	24.0	35.9	17.0	5.4	6.8	4.6	18.6	29.1	12.4
Base cavities	X	Tree with hollow> 30 cm aperture	30	1.4	0.6	1.8	0.2	0.1	0.3	1.1	0.5	1.5

TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Dendrothelms	X	Dendrothelms with >5cm aperture. Water-filled holes in wood.	93	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
Patches with exudates	X	Sap or resin drop: Only a few sap or resin drops (shorter than 30 cm or <6 flows) indicating a minor injury	264	12.1	20.9	6.9	0.9	1.2	0.7	11.2	19.6	6.2
Patches with exudates	X	Heavy sap or resin: fresh heavy flow of sap or resin at least 30 cm long or >5 flows of sap or resin of smaller size	86	3.9	7.7	1.7	0.3	0.2	0.3	3.7	7.4	1.4
Conks of fungi	X(partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies, diameter >5 cm	285	13.0	18.0	10.1	10.1	13.6	8.0	2.9	4.4	2.0
Conks of fungi	X(partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies.	193	8.8	15.1	5.1	7.6	12.8	4.6	1.2	2.2	0.6
Bark characteristics	X	Bark loss: patches with bark loss of at least 5*5 cm mainly caused by felling, natural falling of trees and rock falls	1768	80.7	95.6	72.0	45.9	44.4	46.8	34.8	51.1	25.2
Bark characteristics	X(partially)	Bark burst: black burst of bark at least 2 cm wide often with resin indicating injury/disease	41	1.9	2.7	1.4	0.1	0.1	0.1	1.8	2.6	1.3
Bark characteristics		Gnaw and peeling by ungulates	20	0.9	1.5	0.6	0.3	0.1	0.4	0.6	1.4	0.1

TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Broken tops	X(partially)	Splintered stem: the split-up results in numerous scales (minimum 5) of wood > 50 cm long; caused by another tree fall etc.	70	3.2	4.2	2.6	2.1	3.0	1.5	1.1	1.2	1.1
Cracks	X	Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	4	0.2	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.2
Cracks	X	Cracks: cleft into the sapwood >25 cm long along the stem and at least 2 cm deep in the sapwood	660	30.1	23.7	33.9	7.8	10.4	6.3	22.3	13.3	27.6
Bark characteristics	X	Bark pocket: space between loose bark and the sapwood with a minimum extension of 5*5*2 cm	357	16.3	11.4	19.2	11.9	7.7	14.4	4.4	3.7	4.8
Bark characteristics	X	Bark pocket with mold: same structure and size as Bark loss but with mold.	30	1.4	1.6	1.2	0.8	1.2	0.6	0.5	0.4	0.7
Crown deadwood	X(partially)	Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown.	434	19.8	16.8	21.6	0.0	0.0	0.1	19.8	16.8	21.5
Crown deadwood	X(partially)	Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown.	127	5.8	6.8	5.2	0.0	0.0	0.1	5.8	6.8	5.1

TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Crown deadwood	X(partially)	More than 50% of dead crown: one or more main branches are dead. The living crown seems to be <50% of the former total crown.	163	7.4	8.0	7.1	1.4	2.8	0.5	6.1	5.2	6.6
Broken tops	X	Broken stem: the primary crown is totally absent with or without presence of a secondary crown. Main parts of the tree stem are already dead with decomposing processes.	265	12.1	25.1	4.5	1.7	4.0	0.4	10.4	21.1	4.1
Broken tops	X	Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch results in a severe damage of the main stem.	44	2.0	0.4	3.0	0.0	0.0	0.0	2.0	0.4	3.0
Outgrowth	X	Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark-inhabiting fungi, viruses and bacteria. We recorded areas of canker > 10 cm in diameter	211	9.6	14.7	6.7	0.8	0.7	0.8	8.9	14.0	5.9
Outgrowth	X	Witch broom: dense agglomeration of branches from a parasite or epicormic branching	6	0.3	0.1	0.4	0.0	0.0	0.0	0.3	0.1	0.4

TreM group	Correlation with typology from Larrieu et al. 2018	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Epiphytes	X	Bryophytes developed on >50% of the base or trunk area (height < 1 m)	2762	126.1	57.2	166.6	15.5	11.5	17.9	110.6	45.7	148.7
Epiphytes	X	Ivy developed on > 50% of the base or trunk area (height < 1 m)	18	0.8	0.0	1.3	0.2	0.0	0.4	0.6	0.0	0.9
Epiphytes	X	Mistletoe: presence of a hemiparasitic plants (*e.g.* Viscum spp., Arceuthobium oxycedri, Loranthus europaeus)	40	1.8	3.6	0.8	0.0	0.0	0.1	1.8	3.6	0.7
		SUM	10576	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

Appendix 3: *Comparison of densities of TreM groups between snags and living trees.*