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Consequences of dieback in temperate forests on habitat structure and biodiversity

Jérémy Cours

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UNIVERSITÉ D'ORLÉANS

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UNITÉ de RECHERCHE Ecosystèmes Forestier UR1455 EFNO

THÈSE présentée par :

Jérémy COURS

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Discipline/ Spécialité : **Biologie**

Consequences of dieback in temperate forests on habitat structure and biodiversity

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












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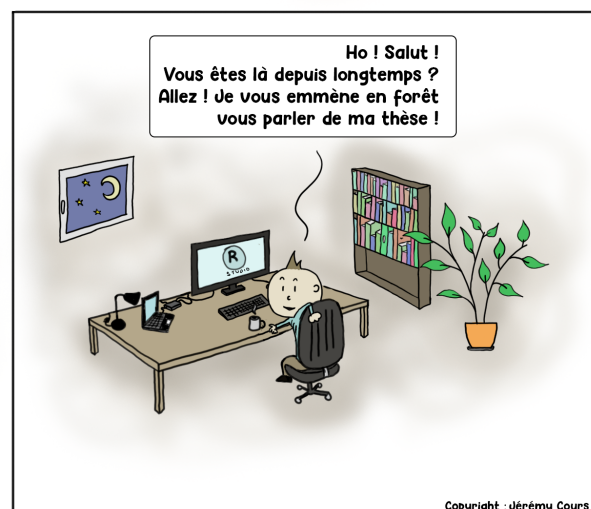
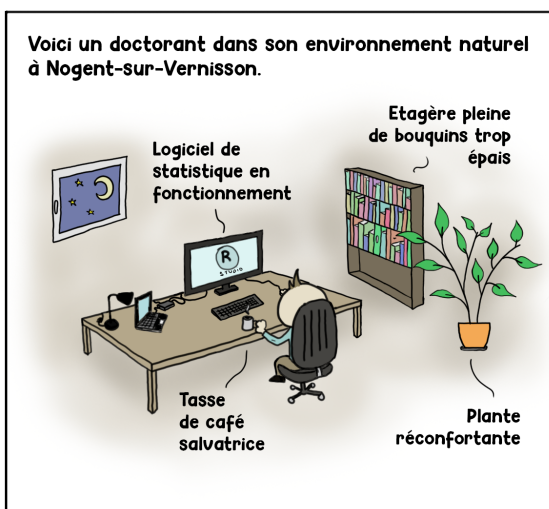
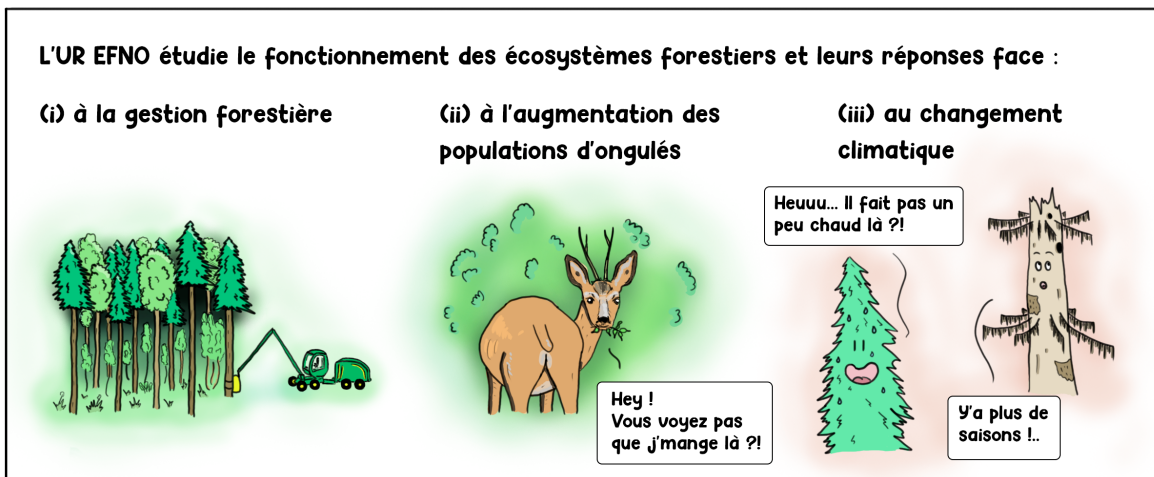
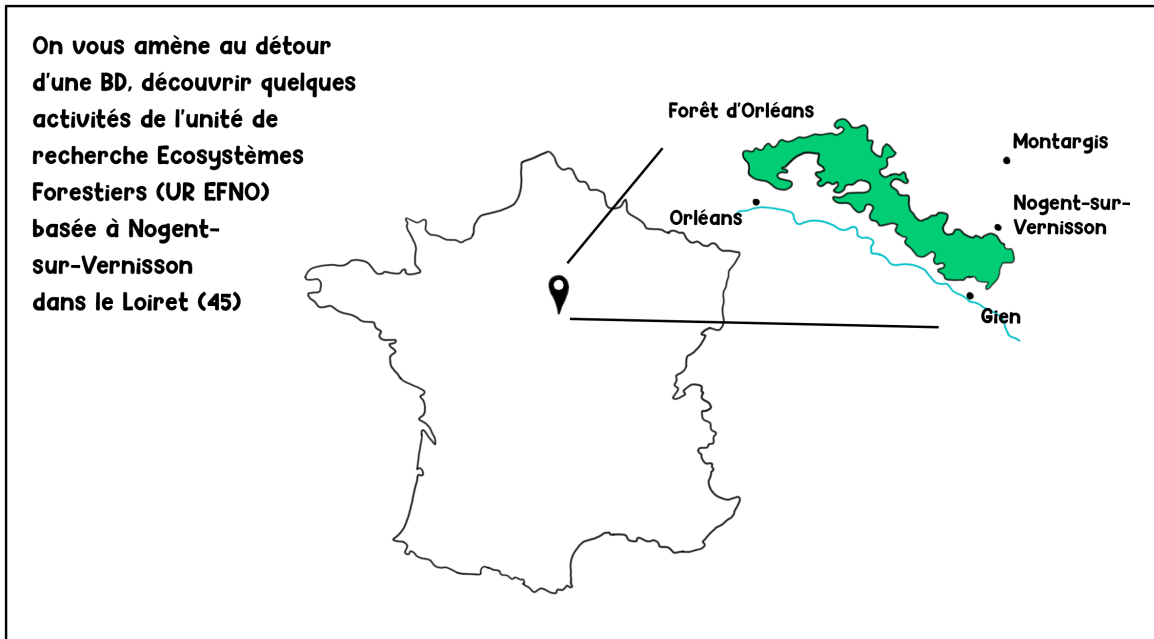
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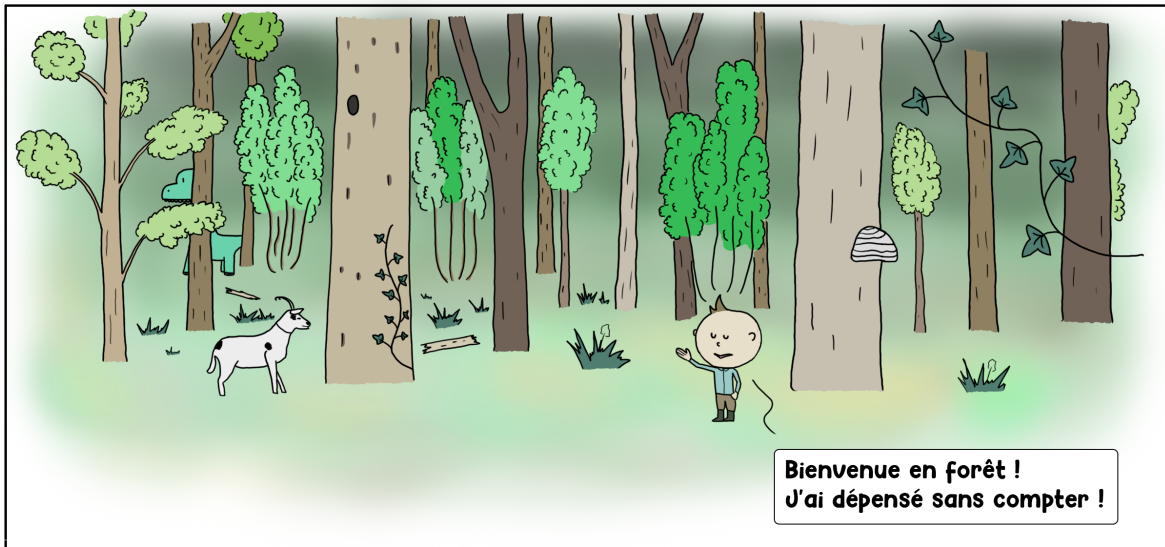
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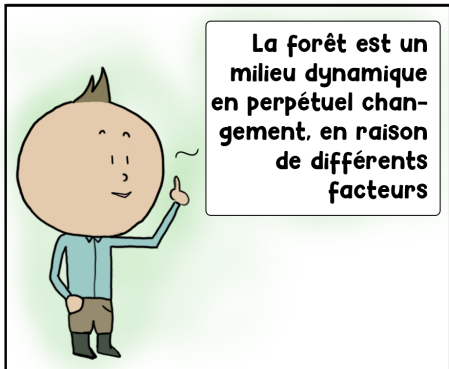
| Consequences of dieback in temperate forests on habitat structure and biodiversity

Graphical abstract





**Bienvenue en forêt !
J'ai dépensé sans compter !**



La forêt est un milieu dynamique en perpétuel changement, en raison de différents facteurs



Les perturbations naturelles, comme les tempêtes et les feux de forêt, en sont de parfaits exemples !



Et elle abrite une foultitude d'habitats, de ressources et de biodiversités !

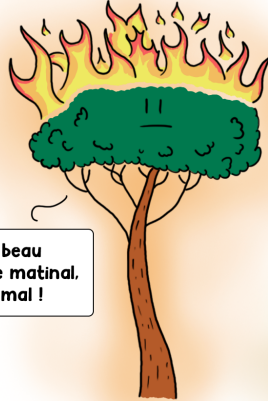
Mais le changement climatique influence de plus en plus ces facteurs de changement :

De plus en plus de sécheresses



J'adore l'eau !
Dans vingt,
trente ans,
y'en aura plus !

De plus en plus de feux



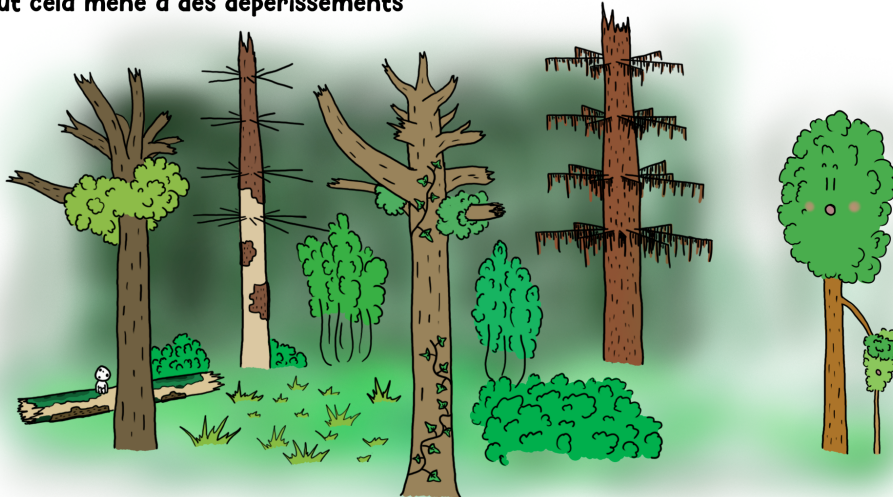
J'ai beau
être matinal,
j'ai mal !

De plus en plus de fortes tempêtes



Je ne me souviens plus très
bien de la soirée d'hier moi !

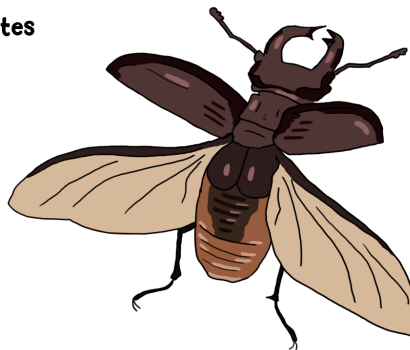
Et tout cela mène à des dépérissements



Ho ! Ne
regarde
pas mon
chéri !

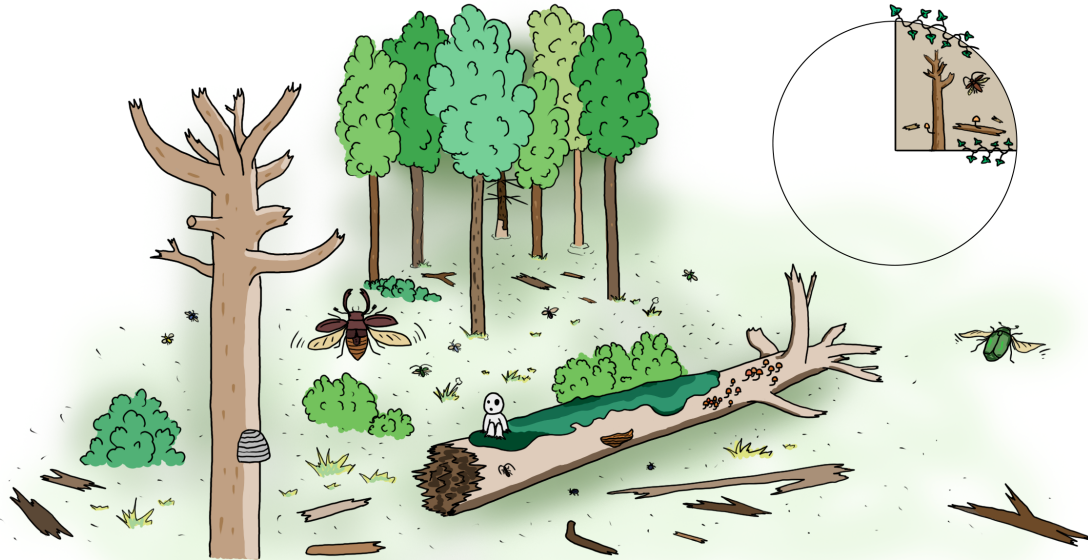
On étudie les conséquences de ces dépérissements sur la biodiversité forestière, principalement par le prisme des coléoptères saproxyliques.

Il s'agit de toutes ces petites bêtes qui ont besoin du bois mort pour se développer.



Hey ! Hey !
Comme moi
le lucane
cerf-volant !

Et il faut savoir que 25% de la biodiversité forestière dépend du bois mort (la biodiversité saproxylique) : des champignons, des insectes (dont beaucoup de coléoptères comme le lucane), etc.



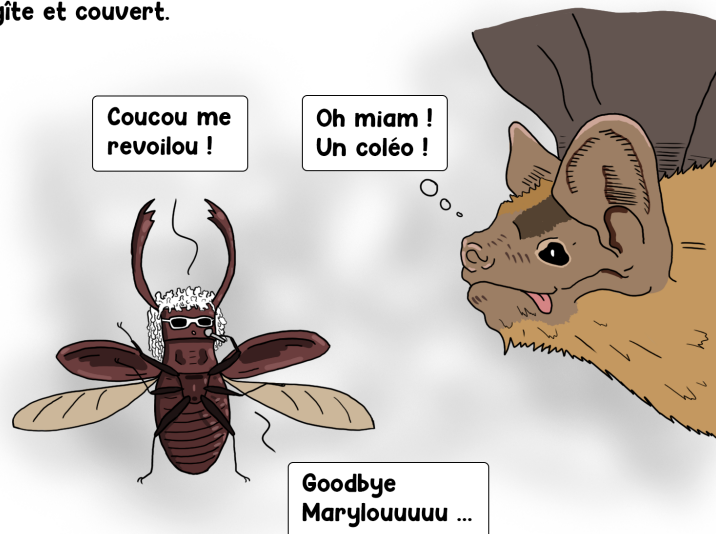
Justement, le dépérissement contribue à l'augmentation en quantité et diversité de cet habitat. En cela, il est un phénomène naturel contribuant au maintien d'une multiplicité d'habitats !

En comparaison, dans les forêts gérées, l'habitat bois mort est une denrée rare



Cette rareté menace les espèces saproxylique dont entre vingt et quarante pourcent sont menacées sur liste rouge en Europe.

Dans ce contexte, nos résultats montrent que le dépérissement peut être bénéfique aux coléoptères saproxyliques, mais aussi aux chauves-souris forestières qui y trouvent gîte et couvert.

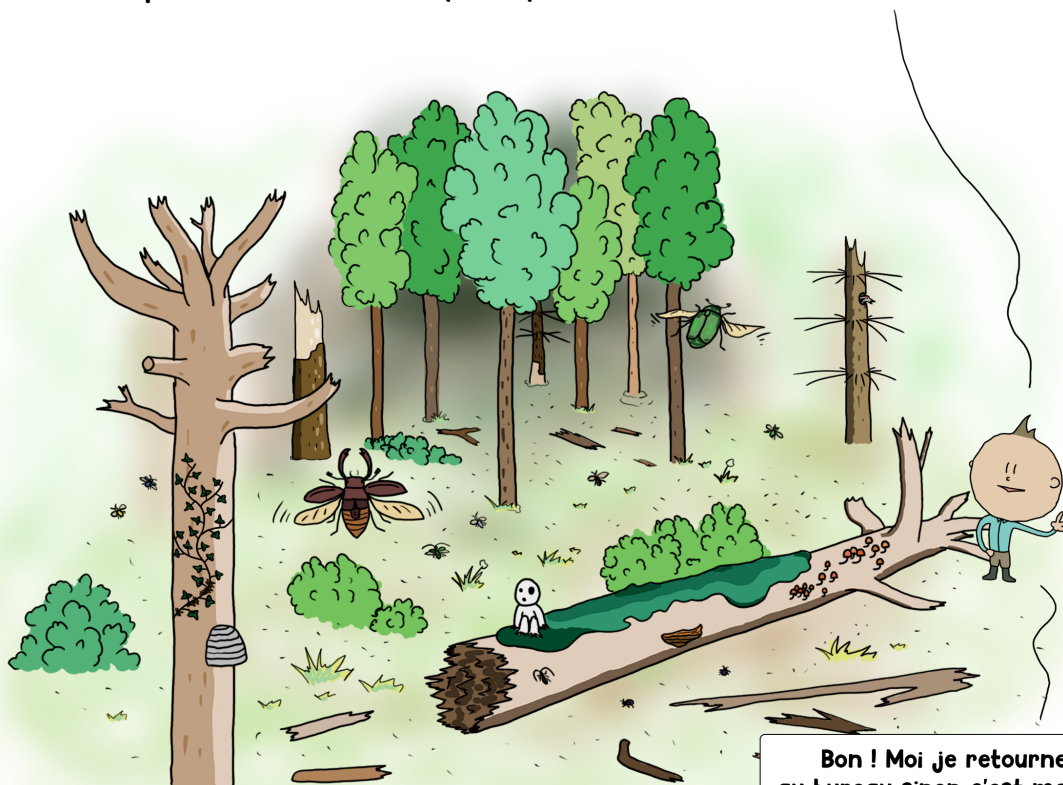


Mais attention, si les dépérissements peuvent avoir des conséquences positives pour une certaine biodiversité, les effets du changement climatique sur les perturbations naturelles pourraient mettre à mal le maintien de l'état boisé dans l'avenir (c'est-à-dire sa résilience), dans certains contextes.



Je vais vous dire
mon secret ...
Je vois des arbres
morts tout le temps
et partout ...

Avant dépérissement, de nombreux facteurs peuvent assurer une meilleure résilience des forêts : diversité de gestions forestières, maintien de réserves forestières non-gérées, etc. Après dépérissement, cependant, le maintien des habitats créés (comme le bois mort) est important puisqu'ils assurent la conservation d'espèces forestières aujourd'hui menacées et potentiellement critiques dans le maintien des forêts futures.



Bon ! Moi je retourne
au bureau sinon c'est ma
thèse qui va dépérir !
Bonne journée !

Copyright : Jérémie Cours

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Encadrants de thèse : Christophe Bouget & Aurélien Sallé Merci à Laura Chevaux pour les jeux de mots !

Scientific production

International scientific publications (in peer-reviewed journals)

Published

- **Cours, J.**, Larrieu, L., Lopez-Vaamonde, C., Müller, J., Parmain, G., Thorn, S., Bouget, C., 2021. **Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests.** *Forest Ecology and Management* 482.
- **Cours, J.**, Sire, L., Ladet, S., Martin, H., Parmain, G., Larrieu, L., Moliard, C., Lopez-Vaamonde, C., Bouget, C., 2022. **Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales.** *Landscape Ecology* 37.

In preparation

- **Cours, J.**, Bouget, C., Leverkus, A.B., Thorn, S., Barsoum, N., Horák, J., Le Souchu, E., Pincebourde, S., Sallé, A., Surviving in a changing world: key contributions of legacies from abiotic disturbances to the resilience of forest arthropod communities. Will be submitted to *Current Forestry Report*.
- **Cours, J.**, Sallé, A., Larrieu, L., Lopez-Vaamonde, C., Müller, J., Parmain, G., Thorn, S., Bouget, C., The living from the dead: changes in taxonomical and functional composition of saproxylic beetles communities following natural disturbances.
- Bouget, C., **Cours, J.**, Larrieu, L., Sallé, A., Speckens, V., Parmain, G., Trait-based response of dead wood and tree-related micro-habitats to dieback in temperate forests. Will be submitted to *Peer Community Journal*.
- Bouget, C., Bard, C., **Cours, J.**, Dieback effects on dead wood: large scale trends from cross-analysis of European forest databases.

Communication at conferences and symposiums

International

- **Cours, J.**, Bouget, C., Leverkus, A.B., Thorn, S., Barsoum, N., Horák, J., Le Souchu, E., Pincebourde, S., Sallé, A., 2022. Surviving in a changing world: key contributions of legacies from abiotic disturbances to the resilience of forest arthropod communities. Presented at the *Forest Disturbance and Ecosystem Dynamics in a Changing World*, Berchtesgaden, Germany. Poster session.
- **Cours, J.**, Bouget, C., Sallé, A., 2021. **Short- and mid-term effects of forest dieback on habitats and resources and on saproxylic beetle communities.** Presented at the *Environmental Research 2021*, [Video](#).

National (France)

- **Cours, J.**, 2021. Effets des dépérissements forestiers induits par les sécheresses sur la biodiversité : le grand inconnu ? Presented at the *Journées scientifiques annuelles (JSA) des sites INRAE du Loiret (45)*, p. 38.
- **Cours, J.**, 2020. Les dépérissements forestiers : un mal pour un bien du point de vue de la conservation de la biodiversité ? Presented at the *Journées scientifiques annuelles des sites INRAE du Loiret*, p. 20.
- **Cours, J.**, Bouget, C., Sallé, A., 2021. Réponses taxonomiques, phylogénétiques et fonctionnelles des coléoptères saproxyliques au dépérissement forestier à l'échelle locale et du paysage dans les montagnes pyrénéennes françaises. Presented at the *14èmes rencontres du GEF - GFPP*, p. 16.

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- Chloé Bard - 2022 (5 months) - Master 2 Mathématiques Appliquées, Statistique, Université d'Orléans - UFR Sciences & Techniques, Orléans. Supervision Christophe Bouget. Effets d'une chronique de dépérissements forestiers sur les conditions d'habitat de la biodiversité, en particulier sur le bois mort.

Video production

- [#Thèse Effets du dépérissement forestier sur l'habitat forestier et sur la biodiversité saproxylique](#)
- [#Thèse - Short- and mid-term effects of forest dieback on saproxylic habitats and beetle communities](#)
- [Conséquences des dépérissements forestiers sur les structures d'habitat et la biodiversité](#)

Table 1 – *My contribution in the different chapters presented in this manuscript. "Maj" = major contribution, "Part" = Major contribution for one part of task, "Sec" = secondary contributions, "AA" = already available*

Part	Title	Idea	Field work	Data treatment	Analysis	Interpretation	Writing
II	Dieback effects on dead wood: large scale trends from cross-analysis of European forest databases	Sec	AA	Sec	Sec	Part	Sec
	Trait-based response of dead wood and tree-related micro-habitats to dieback in temperate forests	Maj	Part	Maj	Maj	Maj	Sec
III	Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests	Part	AA	Part	Maj	Maj	Maj
	The living from the dead: changes in taxonomical and functional composition of saproxylic beetles communities following natural disturbances	Maj	Part	Maj	Maj	Maj	Maj
IV	Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales	Part	AA	Maj	Maj	Maj	Maj
V	Conséquences des coupes sanitaires sur la résilience des écosystèmes forestiers perturbés - une revue de la littérature	Maj	NA	Maj	Maj	Maj	Maj
VI	Surviving in a changing world: key contribution of disturbance legacies to the resilience of forest arthropod communities	Maj	NA	NA	Part	Part	Part

Part I

General introduction

Natural disturbances, forest dieback and biodiversity: an introduction

1.1 Natural disturbances and forest dynamics

1.1.1 Natural forests dynamics: between succession and disruption, equilibrium and non-equilibrium

Forests are highly complex ecosystems filled with many interactions and ruled by numerous processes and mechanisms. Among these processes, two are major components of forest dynamics: the directional succession and disturbances. The temporal dynamics of forest ecosystems was for a long time considered by ecologists as a directional and linear dynamic characterised by plant succession going from an almost bare ground and converging to a static "*forest climax*", a theoretical state of equilibrium marking the end of the forest succession (i.e. *Clement's theory*; Clements, 1916; Kuuluvainen, 2016). The key idea was that any starting point should, under a uniform regional climate, converge to the same equilibrium state (Veblen, 2017). This concept of "climax" was largely based on the paradigm of "*balance of nature*" implying an orderly and harmonious state of nature that all disturbed ecosystems achieve (Wu and Loucks, 1995).

Critics of the Clements' theory and more broadly of the deterministic models of ecosystem dynamics, pointed out the absence of any random factor that would directly affect the succession, such as the dispersion of propagules and site availability through spatial and temporal scales (Veblen, 2017). Indeed, this equilibrium view of nature was counterbalanced by many non-equilibrium factors. Unpredictability, instability and stochasticity are as many factors interacting and leading to non-equilibrium dynamics of ecosystems (Mori, 2011; Wu and Loucks, 1995). For instance, the aforementioned "*climax*" itself is a non-equilibrium state due to historic climatic changes and subsequent changes in disturbances over time (i.e. temporal non-equilibrium; Sprugel, 1991) and is actually highly scale-dependent (such as concepts of landscape equilibrium; Pickett and White, 1985; Turner, 2010). Likewise, the heterogeneity of ecosystems over space also responds to non-equilibrium dynamic systems (i.e. spatial non-equilibrium; Mori, 2011). As a consequence, the shift from the equilibrium to the non-equilibrium paradigm induced a shift in perception of forest dynamics: from the directional perspective of development to multi-cyclical models, composed of interacting time and spatial cycles (Kuuluvainen, 2016). Disturbances are one of the main mechanisms of non-equilibrium state of terrestrial ecosystems (Kuuluvainen, 2016; Pickett and White, 1985; Pulsford et al., 2016). Nonetheless, although disturbances can be highly random processes, an equilibrium can be observed in the overall patterns of natural disturbance regimes. The majority

of disturbances occurring in a specific area are enclosed in a multidimensional space in which each dimension is a characteristic of the whole disturbance (i.e. the disturbance regime). The limits of this multidimensional space are called the "*natural range of variation*" (Donato et al., 2020; Landres et al., 1999).

1.1.2 Ecological importance of natural disturbances

We use here the term "disturbance" as defined by Pickett and White (1985): "*any relative discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment*". Disturbances can be qualified as either natural or anthropogenic. Natural disturbances take place without direct human influence, while anthropogenic disturbances are the direct result of human activity (e.g., forest management). This dichotomy can be considered as an oversimplification since the two causes can be difficult to separate and interact with each other. For example, wildfires, a natural disturbance are also mainly due to human activity (Ne'eman et al., 2004). Nevertheless, for the sake of convenience, we will use the terms natural and anthropogenic as defined above. Disturbances are characterised by several features: type, severity, frequency, spatial extent, distribution, synergism, rotation periods, which constitute their disturbance regime (Mori, 2011; Pickett and White, 1985; Veblen et al., 1994).

Natural disturbances have a large ecological importance. They can reset local communities, disrupt ecological successions, create new resources and, ultimately shape the structure and functioning of ecosystems. They ensure the maintenance of a high spatial and temporal heterogeneity of habitats and resources in the landscape (Pickett and White, 1985). Depending on their frequency, severity or spatial extent, they can lead to more or less extended ecological changes. Stand-replacing disturbances, such as a large wildfire, can completely change the environmental conditions over large spatial scales; while partial and gap disturbances, such as tree infestation by fungi or insects, would only affect very local conditions (Kuuluvainen, 2016; Swanson et al., 2011). Over time, the occurrence of partial and gap disturbances together with stand-replacing ones, in interaction with environmental conditions (e.g., topography, vegetation, etc.), result in a high heterogeneity of habitats and resources (Swanson et al., 2011; Turner et al., 1999). Even a very large disturbance can lead to a high spatial heterogeneity due to differences in severity and pre-disturbance conditions across the landscape (Turner, 2010). Therefore, forest landscape patterns worldwide are largely influenced by disturbance regimes (Turner et al., 1997, 1999). For example, the 1988 fires in Yellowstone National Park resulted in a heterogeneous vegetation composition across the landscape, due to patches of unburnt vegetation and different recolonisation patterns related to the fire severity gradient (Turner et al., 1997, 1999).

Each disturbance leaves in the environment peculiar biologically-derived materials or exerts selective pressures that may persist in the ecosystem or at the landscape level (Franklin et al., 2000; Johnstone et al., 2016). These material and informational imprints persisting in ecosystems after a disturbance are named "*disturbance legacies*" (Franklin et al., 2000; Johnstone et al., 2016). The nature, amount and diversity of disturbance legacies depend on disturbance regime: windstorms produce large amounts of both snags and logs, wildfires lead to large amounts of charred dead wood but lower amount of soil organic layer, etc. (Swanson et al., 2011). As a result, disturbances can be seen as "*editors*" as "*they selectively remove or modify elements of an ecosystem while leaving others intact*" (Franklin et al., 2000). Disturbance legacies played key roles in recovery processes after various major disturbance events during the 1980s and early 1990s (e.g., the Mount St. Helens eruption in 1980 or the Yellowstone fires in 1988 mentioned above Turner, 2010). The diversity of disturbance legacies, facilitated ecosystem recovery processes and even promoted biodiversity (Franklin et al., 2000).

Johnstone et al. (2016) proposed to divide disturbance legacies in two categories: material and information legacies. Material legacies are all substrates (e.g., dead trees, individual survivors, nutrient,

litter, seeds, etc.) that are present in the ecosystem after the disturbance. Information legacies are the set of adaptive traits borne by species in a community or population that have been selected by disturbance regimes. As major ecological filters, disturbances exert important evolutionary pressures. In response to particular historical disturbance regimes, many species had developed specific adaptations. For instance, resprouting, serotiny, heat-shock triggered germination, thick bark, etc. could be seen as many responses to particular fire regimes, with some more adapted to surface-fire regime and other to crown-fire regime (Batllori et al., 2017, 2019; Dale et al., 2001; Keeley et al., 2011; Pausas et al., 2004).

1.1.3 Drivers of natural disturbances

Different forest ecosystems are influenced by different sets of natural disturbance regimes. For example, boreal forests are modulated by infrequent large wildfires while temperate Atlantic forests are rather modulated by large windstorms (Kulakowski et al., 2017; Schelhaas et al., 2003). By contrast, tropical forests would be much more modulated by individual tree mortality (Pickett and White, 1985). As a consequence, natural disturbances are greatly mediated by biogeographic processes, such as climate and topography. Fires are preponderant in ecosystems experiencing summer droughts while windstorms and avalanches are major factors of forest dynamic in mountain areas (Kulakowski et al., 2017; Schelhaas et al., 2003; Seidl et al., 2017). Nonetheless, their effects also depend on local environmental conditions pre-disturbance. For instance, certain plant species are fire-prone and could facilitate fires (Ormeño et al., 2009; Varner et al., 2015); trees have to reach a minimal size to be affected by windstorm (Jahani and Saffariha, 2021). Likewise, certain forest successional stage are more fire prone than others e.g., the older stands in 1988 Yellowstone fires (Turner et al., 1999).

Disturbances also interact between themselves. These interactions could be antagonistic, additive or synergistic. For instance, as aforementioned, droughts could facilitate subsequent insect outbreak and wildfire (Batllori et al., 2017; Seidl et al., 2017). Likewise, windstorm could facilitate subsequent insect outbreaks (Seidl et al., 2017; Thorn et al., 2017). The compound effect due to the addition and interaction between several natural disturbances can lead to specific ecological outcomes, different from the effects of the disturbances alone (Batllori et al., 2017, 2019; Burton et al., 2020; Paine et al., 1998). For example, two consecutive wildfires result in significantly less dead wood than a single fire (Batllori et al., 2019).

1.1.4 Natural disturbances and the forest dieback concept

Disturbances can affect tree vigour and survival over large spatial scales, with prolonged effects. The phenomenon of more or less progressive tree loss of vigor and death, from the tree level to landscape scale is called "*forest decline*" or "*forest dieback*". Historically, both terms were popularized during the 1980s in response to the inexplicable loss of vigour and health of trees and stands in the Black forest of western Germany and in the Vosges montane forests in eastern France (the so-called "*Dépérissement forestier*" in French and "*Waldsterben*" in German; Ciesla and Donaubauer, 1994; Nageleisen et al., 2010). Terms *forest decline* and *forest dieback* described two stages of the same process: decline is defined as *the loss of vigour of a forest stand* while dieback could be considered as *the further progression of decline which leads to stag-headedness of many trees* (Ciesla and Donaubauer, 1994). The concepts of forest decline and dieback were then considered through an anthropogenic vision: the phenomenon is a disease displaying symptoms and not an ecological process (Ciesla and Donaubauer, 1994). Later, however, Mueller-Dombois (1986; 1992) described the phenomenon of forest decline and dieback not as a disease but as an integral part of forest dynamics, making the connection with studies on natural disturbances (Ciesla and Donaubauer, 1994; Pickett and White, 1985). In the manuscript we only use the term *forest dieback* for convenience. Therefore, we described the forest dieback as the phenomenon of more or less progressive death of trees through the succession of different factors: predisposing (e.g., sandy soils), inciting (e.g., drought) and contributing factors (e.g., pest outbreak) (Ciesla and Donaubauer, 1994;

Manion, 1981; Nageleisen et al., 2010). In this process, natural disturbances like droughts, windstorms or wildfires, generally act as inciting factor, triggering the dieback process. In this manuscript, I will use this definition of forest dieback, i.e. an ecological process leading to tree death following a disturbance.

1.1.5 Natural disturbances and human influence on forest dynamics

Historically, forest management has largely interfered with natural disturbances to maintain the ecological services provided by managed forests to human societies. For example, forest management tend to prevent wildfires or limit their severity and spatial extent when it aims to produce wood products from living trees. Nonetheless, forests can also be burnt for agricultural purposes. As a consequence, many of the tree species found in current forests are the result of centuries (or even millennia) of human selection: some were disadvantaged while others were selected for food and fibre (e.g., *Castanea* and *Juglans* species; Conedera et al., 2017) or took advantage of anthropogenic disturbance regime (e.g., the fire-suppressed management in the United States; Friedman and Reich, 2005). Therefore, as an "editor", forest management is considered to be a type of disturbance, retaining distinct legacies such as tree species with peculiar characteristics (i.e. the anthropogenic disturbances).

As a consequence, the history of anthropogenic disturbances has strongly affected the forest dynamics for very long time. For instance, several parts of the Amazon forest have been influenced by past human activities (McMichael, 2021). Likewise, in regions with a long history of human activity, forest compositions and functioning is much more the result of past and current land use and anthropogenic disturbances than of climate and natural disturbances (Bebi et al., 2017; Chevaux et al., 2022; Conedera et al., 2017; Kulakowski et al., 2017; Sabatini et al., 2018; Sommerfeld et al., 2018; Vacchiano et al., 2017).

In addition to plant composition, forest management has large consequences on habitats and substrates found in forests. For instance, dead wood, which is generally an important resource in natural forest, is very scarce in managed forests. In a study on Fennoscandian forests, Siitonen (2001) showed that managed forests have globally 90% to 98% reduction of dead wood amount. Yet, the quantity and diversity of dead wood in natural forest accounts for almost 25% of forest biodiversity (i.e. the saproxylic biodiversity; Stokland et al., 2012; Ulyshen, 2018). Likewise, intensively managed forests shelter a lower diversity of tree-related microhabitats (i.e. the microhabitats borne by living and dead trees; Larrieu et al., 2018) than unmanaged or extensively managed ones (Asbeck et al., 2022; Larrieu et al., 2012).

Summary: We have described the main mechanisms of forest dynamics in which natural disturbances are a main component. Their regimes (i.e. severity, frequency, spatial extent, etc.) strongly affect the spatial and temporal dynamics of forests, leading to high heterogeneity of habitats and resources. The material remaining or transformed after a natural disturbance is called *biological legacies* and bears an important part of the resilience of the ecosystem after the disturbance. Furthermore, natural disturbances are an important evolutionary force and have selected adaptive traits among ecological communities. Nevertheless, natural disturbance regimes have interacted extensively with human pressures over the past centuries (or even millennia) and have thus been strongly modified worldwide.

Résumé : Nous avons décrit les principaux mécanismes de la dynamique forestière dans laquelle les perturbations naturelles sont une composante principale. Leurs régimes (c'est-à-dire la sévérité, la fréquence, l'étendue spatiale, etc.) affectent fortement les dynamiques spatiales et temporelles des forêts, conduisant à une grande hétérogénéité des habitats et des ressources. Les matériaux restants ou transformés après une perturbation naturelle sont appelés *héritages biologiques* et porte une part importante de la résilience de l'écosystème après la perturbation. En outre, les perturbations naturelles constituent une force évolutive importante et ont sélectionnés des traits d'adaptation parmi les communautés écologiques. Néanmoins, les régimes de perturbations naturelles ont largement interagi avec les pressions humaines au cours des derniers siècles (voire millénaires) et ont donc été fortement modifiés dans le monde entier.

1.2 Current and predicted effects of climate change on natural disturbance regimes and cascading effects on forest dynamics

1.2.1 Current and predicted effects of climate change on natural disturbance regimes

Overall, climate change is affecting the regime of most of forest natural disturbances (Dale et al., 2001; Seidl et al., 2017). For example, as a result of rising temperatures and change in precipitation patterns, droughts are becoming continuously more intense, more frequent and more spatially extended (McDowell et al., 2020; Samaniego et al., 2018). As a result, droughts have recently become the main forest disturbance in Europe (Senf and Seidl, 2021b). Likewise, climate change increases the frequency and spatial extent of forest fires (Cattau et al., 2020; Whitman et al., 2022) and is expected to have an overall positive effect on major insect pests, such as bark beetle (Bentz et al., 2010; Hlásny et al., 2021b). The effects of climate change on windstorms are much more limited, but windstorms should also increase under particular conditions and in particular areas (i.e. warmer and wetter climate; Schelhaas et al., 2003; Seidl et al., 2017). These changes in natural disturbance regimes are called "regime shifts" and they are expected to have significant cascading effects on forest ecosystems worldwide (Turner, 2010).

1.2.2 Cascading effects of changing natural disturbance regimes on forest dynamics

Trees are sessile and perennial organisms, which are unable to change their spatial distribution very quickly in response to an environmental change. As a result, the pace of climate change is currently significantly faster than plant species dispersal ability over latitudinal and altitudinal gradients, thus creating a disequilibrium between vegetation composition and their environment (Bertrand et al., 2011; Thom et al., 2017b). This disequilibrium puts at stake the future provision of forest ecosystem services since it would create a *resilience debt* or an *extinction debt* (Johnstone et al., 2016). The concept of resilience debt describes the phenomenon of background changes in environmental conditions without any change in species communities (i.e. *the misalignment of information legacies and disturbance impacts*; Johnstone et al., 2016), resulting in a loss of resilience capacities. At the extreme, extinction debt predicts the future extinction of species that persist in an ecosystem when their habitat has been lost or is largely degraded (Kuussaari et al., 2009). Ultimately, these debts would be paid at the time of a disturbance leading to unforeseen ecological trajectories. Natural disturbances would consequently catalyze significant changes in ecological communities (Turner, 2010), which may lead to better adaptations to the new climate conditions. In a simulation study, Thom et al. (2017b) showed that natural disturbances should fasten the adaptation towards new tree species composition at the landscape level. Likewise, in a temporal survey of vegetation colonisation within forest gaps caused by windstorms, Dietz et al. (2020) showed that the disturbance promoted the thermophilization of plant communities. Actually, forest ecosystems in a changing world could take several post-disturbance trajectories: (i) the resilience (no change in structure and composition), (ii) restructuring (structure changes but composition does not), (iii) reassembly (composition changes but structure does not), (iv) replacement (structure and composition both change), and (v) complete ecological shift leading to non-forest (Seidl and Turner, 2022).

Climate change, through shifts in disturbance regimes, is already affecting forest ecosystems. Over the last decades, an overall decline of tree crown conditions has been reported worldwide (Carnicer et al., 2011; Hammond et al., 2022; McDowell et al., 2018; Senf et al., 2018; Sommerfeld et al., 2018). Shifts in drought regimes resulted in overall increase in crown dieback and tree mortality worldwide (Allen et al., 2015; Carnicer et al., 2011; Hammond et al., 2022; Sommerfeld et al., 2018; Taccoen et al., 2019, 2022). The increase in vapor pressure deficit (VPD) over the last three decades has also been associated with a reduction in global vegetation growth (Yuan et al., 2019). The increase in the frequency and spatial extent of dieback and decline events will likely have significant impacts on forest demography and age structure (Turner et al., 2021). In a simulation, McDowell et al. (2020) predicted an increase of young forest

areas coupled with a significant decrease in areas of old-growth forests (i.e. more than 140 years old). In this study, droughts were identified as a major factor affecting forest resilience, as they increased tree mortality while reducing tree growth and recruitment. Shifts in disturbance regimes may then affect forest resilience capacities, while natural disturbance events could be catalysts for forest change and adaptation (e.g., Turner et al., 2021; Woolman et al., 2022).

Summary: We have listed the effects of climate change on the main natural disturbances in forest ecosystems. In fact, climate change is expected to (and has already) intensified the main natural disturbance regimes, such as droughts, wildfires or bark beetle outbreaks. These changes in disturbance regimes are called *regime shift*. The latter would affect forest ecosystems whose structure is based on long-lived, immobile organisms such as trees. Trees are already experiencing the effects of climate change, with widespread tree and crown mortality, mainly due to drought events. Natural disturbances could be a catalyst for ecosystem change and adaptation, while regime shift could, at the same time in extreme situations, induce irreversible shifts in ecological trajectories towards non-forest ecosystems.

Résumé : Nous avons énuméré les effets du changement climatique sur les principales perturbations naturelles dans les écosystèmes forestiers. En fait, le changement climatique devrait (et a déjà) intensifié les principaux régimes de perturbation naturelle, comme les sécheresses, les incendies de forêt ou les épidémies de scolytes. Ces changements dans les régimes de perturbation sont appelés *regime shift*. Ce dernier affecterait les écosystèmes forestiers dont la structure repose sur des organismes immobiles et à longue durée de vie tels que les arbres. Les arbres subissent déjà les effets du changement climatique, avec une mortalité généralisée des arbres et des couronnes, principalement due à des épisodes de sécheresse. Les perturbations naturelles pourraient être un catalyseur de changement et d'adaptation pour les écosystèmes, tandis que le changement de régime pourrait, parallèlement dans des situations extrêmes, induire des modifications irréversibles des trajectoires écologiques, vers des écosystèmes non forestiers.

1.3 Dieback and biodiversity dynamics: a poorly understood response

1.3.1 Biodiversity and forest ecosystems: concepts and theories

Forests, as complex ecosystems, harbour a large diversity of living organisms. For example, almost 12,000 species from most of living kingdoms have been described in the Bialowieza forest (Vallauri and Neyroumande, 2009). This diversity, called *biodiversity* include *the variability among living organisms from all sources including [. . .] ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems* (United Nations, 1992). In this thesis, I will use the term biodiversity to refer to (i) species richness or also taxonomic diversity (i.e. the diversity of species), (ii) functional diversity (i.e. the diversity of traits carried by species), and (iii) the phylogenetic diversity (i.e. the diversity of parental relationships between species on the phylogenetic tree). In addition, biodiversity can be divided into several components, depending on the spatial scale considered: (i) α -diversity (i.e. the coexisting diversity at the habitat or site level, see chapters 5, 6 and 7), (ii) β -diversity (i.e. differences in species composition between habitats and sites, see chapters 5, 6), and (iii) γ -diversity (i.e. the total diversity across a landscape, which is the result of the combination of α -diversity and β -diversity, see chapters 4 and 6). Communities are pools of interacting species within a same environment. In addition to evolutionary processes, community assembly is regulated by three major mechanisms (HilleRisLambers et al., 2012; Janssen, 2016): (i) dispersal capacities and chance for a species to reach a particular environment, (ii) abiotic filters by which a species can maintain itself, grow and reproduce because it has found a suitable environment, and (iii) biotic filters through which a species may or may not persist because of the interactions it has with other species present.

Several theories and hypotheses have been proposed to explain local patterns of biodiversity. In ecology, the *species-area relationship* is considered a fundamental law to explain biodiversity patterns (Lomolino, 2000; MacArthur and Wilson, 1967). It predicts that over a gradient of ecosystems of

increasing size, the species diversity in each of these ecosystems increase along the gradient, rapidly at the beginning and more and more slowly as one moves along the gradient (Godeau et al., 2020; Lomolino, 2000). The main result of this relationship is that as habitat size increases, so does species diversity, through a power function (also called *Arrhenius model*; Lomolino, 2000). This relationship was developed by MacArthur and Wilson (1967) in the *theory of island biogeography*. The latter predict that as island size increases, so does species diversity. Furthermore, the species richness on an island is the result of an equilibrium between immigration of new species from a mainland (i.e. "*primary faunal source area*") and species extinction. Species gain is due to higher immigration than extinction rates, while species loss is due to higher extinction than immigration. Furthermore, the immigration of new species is a function of the distance between the island and the mainland. As a result, the theory of island biogeography allows to explain why certain islands are more populated than others as a function of island size and distance to mainland. Extended, the theory allows to understand the distribution of species richness between separated patches of habitats in non-island systems (e.g. mountains, forests, trees, etc.; Harris, 1984; Janssen, 2016). This framework is also referred as the "*habitat patch concept*" (Fahrig, 2013). Nonetheless, Fahrig (2013) showed that patch size and isolation effects are actually driven by an underlying process: the sample area effect for which species diversity is the function of both patch size and the quantity of surrounding patches. As a result, species diversity globally depends on the total amount of habitat in the "*local landscape*" (i.e. *the area within an appropriate distance of the sample site*; Fahrig, 2013). This framework is then referred as the "*habitat amount hypothesis*" (Fahrig, 2013; Seibold et al., 2017). The hypothesis implies that species do not just live in a single habitat patch, but actually live in a sum of patches that are close enough to each other to allow species to move between them to meet their needs. In parallel, since we are not considering true islands within an ocean, the matrix (i.e. non-habitat area surrounding habitat patches) largely affects species dispersal by its quality; e.g., for an individual to cross a length of forest separating it from a suitable habitat does not represent the same choice as to cross a meadow of the same length (Taylor et al., 1993). Therefore, each studied community has its own local landscape, based on different dispersal capacities and different study contexts. This optimal spatial scale to study the response of a community to habitat amount is called the "*scale of effect*" (Fahrig, 2013; Seibold et al., 2017). In this manuscript, I considered these landscape considerations of community distribution in response to forest dieback in the chapters 6 and 7.

Once a species has arrived in a particular habitat, it needs particular environmental conditions to maintain, grow and eventually reproduce (i.e. the abiotic filter; HilleRisLambers et al., 2012). All these abiotic conditions necessary for the survival of a species are called the "*ecological niche*" (Chase and Leibold, 2003; Grinnell, 1917; Hutchinson, 1957). Therefore, the species' ecological niche can be considered as an "*n-dimensional hypervolume*" in which each dimension constitutes a singular ecological requirement (i.e. the "*fundamental niche*"; Chase and Leibold, 2003; Hutchinson, 1957). In addition, the coexistence of a species with a myriad of others generally lead to the contraction of its ecological niche in a given environment (e.g. due to competition, predation etc.), but could also lead to an expansion (e.g. due to facilitation interaction). The result of changes in ecological niche due to the interactions between species is called the "*realized niche*" and could result in species exclusion (i.e. biotic filter and partly associated to the "*competitive exclusion principle*"; Chase and Leibold, 2003). The concept of ecological niche implies that an increasing diversity of habitats and resources in an ecosystem leads to an increasing range of environmental conditions that ultimately leads to an increasing species diversity (i.e. the "*habitat-heterogeneity hypothesis*"; Seibold et al., 2016). In contrast, it has also been proposed that an increasing amount of resource lead to higher available energy for individuals. The increase in individuals subsequently lead to higher species diversity (i.e. the "*species-energy hypothesis*" and the "*more-individuals hypothesis*"; Müller et al., 2018; Seibold et al., 2016). The habitat-heterogeneity hypothesis suggests that species diversity is directly regulated by habitat diversity, while the species-energy hypothesis suggests that species diversity is indirectly regulated by the amount of resources. I specifically investigated the direct effects of natural disturbances and resulting forest dieback on microhabitats and

resources in the chapters 3 and 4. I also questioned the cascading effects of forest dieback on biodiversity through changes in habitat conditions in the chapters 5 and 6.

1.3.2 Biodiversity at stake in the Anthropocene

We are living in a period of rapid changes in climate and human land use, in a world so dominated by human pressures that geologists have proposed to divide it into a new geological era: the *Anthropocene* (Lewis and Maslin, 2015; Newman, 2019). In parallel to these rapid changes, an ongoing biodiversity crisis is declared leading to the premises of the Sixth Mass Extinction (Cowie et al., 2022; Dirzo et al., 2014). Authors talk about *defaunation* (Dirzo et al., 2014) and *biotic homogenisation* due to the loss of specialist species (Clavel et al., 2011; Devictor et al., 2008). In that respect, arthropods (and especially insects) appears highly at stake with many warnings from the scientific community concerning their large decline (Cardoso et al., 2020; Hallmann et al., 2017; Jactel et al., 2020; Seibold et al., 2019; Van Klink et al., 2020). In forest, they represent the richest taxonomic group with almost 70% of species among all known organisms (50% for insects; Wermelinger, 2021). In forests, the decrease appears to be smaller than in grassland (Seibold et al., 2019) but still significant (Evans et al., 2022; Homburg et al., 2019). These declines in arthropod communities likely result from combined effects of habitat loss (Seibold et al., 2015), land-use intensification (especially agriculture; Outhwaite et al., 2022; Seibold et al., 2019) and climate change (Lister and Garcia, 2018; Outhwaite et al., 2022). For instance, saproxylic biodiversity (i.e. biodiversity related to dying and dead trees, for at least part of their life cycle), represented by many insect species and accounting for nearly 25% of the boreal and temperate forest biodiversity (Stokland et al., 2012) is threatened in managed forests due to the loss of dead wood habitat. As a result, about 20-30% of European saproxylic beetle species are considered threatened in the Red List (Calix et al., 2018; Seibold et al., 2015).

Therefore, in this period of rapid global changes, arthropods appear to be a relevant ecological group to study the effects of these changes e.g., saproxylic insects in a generally managed forest setting. They represent the richest taxonomic group in forest (Wermelinger, 2021), an incredible biomass vital to forest food chains, a key contributor to forest ecosystem function due to their very diverse functional traits.

1.3.3 The acknowledged consequences of diebacks on forest biodiversity

According to current knowledge, natural disturbances and the resulting forest diebacks affect biodiversity through several mechanisms. Firstly, the "*intermediate disturbance hypothesis*" predict that the highest biodiversity is found at intermediate-disturbance regimes due higher species coexistence and lower competition (Connell, 1978; Pulsford et al., 2016; Roxburgh et al., 2004). At a landscape scale, as aforementioned, natural disturbances promote habitats and create heterogeneity (Kulakowski et al., 2017; Schoennagel et al., 2008; Turner, 2010). This spatial heterogeneity, and the amount of newly habitat created in the landscape, affect species dispersal and underlying colonisation and extinction patterns (see chapters 6 and 7; Fahrig, 2013; Georgiev et al., 2022; MacArthur and Wilson, 1967; Tatsumi et al., 2020; Winter et al., 2017). Furthermore, in a managed forest landscape, dieback could create new habitats and resources typical to old-growth forests, such as dead wood and related microhabitats (see chapters 3 and 4) (Donato et al., 2016; Swanson et al., 2011; Thorn et al., 2017; Waldron et al., 2013).

At more local scale, natural disturbances induce changes in communities through changes in environmental conditions. In a meta-analysis, Thom and Seidl (2016) showed that natural disturbances lead to an increase in overall species richness of almost 35%. Due to the increase in dead wood amount and diversity and changes in tree-related microhabitats, forest dieback has overall positive effects on saproxylic guilds (see chapters 5 and 6; Beudert et al., 2015; Boucher et al., 2016; Kozák et al., 2021; Viljur et al., 2022). Likewise, the increase in habitat trees has generally favoured forest bat species and some specialist bird species (e.g., the black-backed woodpecker (*Picoides arcticus* Nappi and Drapeau, 2009) (Kortmann

et al., 2018b; Viljur et al., 2022) while canopy opening favored edge-space bat species (Erasmey et al., 2021; Mehr et al., 2012; Rachwald et al., 2022; Viljur et al., 2022). In contrast, species living in habitats degraded by disturbance generally decline in cascade (e.g., decrease in eucalyptus hollow-bearing trees after fire leading to decreased species richness of arboreal marsupials; Bowd et al., 2021a). In addition, the canopy opening triggered by tree death is also beneficial for many species associated with open-areas resources. For example, bees, wasps and hoverflies generally benefited from natural disturbance and the resulting forest dieback (Beudert et al., 2015; Moretti et al., 2004; Viljur et al., 2022). Most of studies on the consequences of forest diebacks on biodiversity, investigated the impacts of wildfires, windstorms and insect outbreaks. By contrast, drought effects on forest insect communities has received relatively little attention, although this disturbance appears a major XXIst century's disturbance (Senf and Seidl, 2021a). Yet, drought appears to have an important impact on several guilds: it has negative effects on soil biodiversity for example (Lindberg et al., 2002; Peguero et al., 2021; Wehner et al., 2021) or it significantly affects assemblages of forest ground-dwelling carabid (Evans et al., 2022; Jouveau et al., 2022).

Summary: We have defined the term *biodiversity* and listed and defined its different component (i.e. the taxonomic, functional and phylogenetic diversities on the one hand, and α , β and γ -diversities on the other). In addition, we have listed and defined most of theories and hypothesis explaining biodiversity patterns in the framework of the thesis. We have also contextualised biodiversity issues in the Anthropocene, the premises of the Sixth Mass Extinction and the decline of arthropods. Therefore, we stressed the importance of studying arthropod responses to changing environmental conditions (e.g., forest dieback). Subsequently, we described the known consequences of forest dieback on biodiversity and some underlying mechanisms.

Résumé : Nous avons défini le terme de biodiversité et énuméré et défini ses différentes composantes (c'est-à-dire les diversités taxonomique, fonctionnelle et phylogénétique d'une part, et les diversités alpha, beta et gamma). En outre, nous avons répertorié et défini la plupart des théories et hypothèses expliquant les modèles de biodiversité dans le cadre de la thèse. Nous avons également contextualisé les questions de biodiversité dans l'Anthropocène, les prémisses de la sixième extinction de masse et le déclin des arthropodes. Par conséquent, nous avons souligné l'importance d'étudier les réponses des arthropodes aux changements des conditions environnementales (par exemple, le dépérissement des forêts). Par la suite, nous avons décrit les conséquences connues du dépérissement forestier sur la biodiversité et certains mécanismes sous-jacents.

1.4 Problem, hypotheses and objectives of the thesis

Despite a large number of studies, the subject of the forest dieback consequences on biodiversity still has many frontiers of knowledge. A major knowledge gap concerns the cascading effects of forest dieback on biodiversity mediated by habitat changes. Similarly, the landscape effects of forest dieback on biodiversity are another gap in current knowledge. Moreover, there is also a current gap of knowledge regarding global surveys on the effects of forest dieback on habitat, such as dead wood and tree-related microhabitats, even more so after drought-induced dieback. Consequently, in this manuscript we seek to better understand the consequences of temperate forest dieback on habitat structure and biodiversity. We specifically studied the saproxylic beetle guild because we expected an increase in the amount and diversity of dead wood and tree-related microhabitats after dieback. We expected an increased abundance and diversity of saproxylic beetles as the result of the increase in habitat diversity (*habitat-heterogeneity hypothesis*) and resource quantity (*species-energy hypothesis*). Similarly, we expected a much higher response of saproxylic beetles to a large spatial rather than local increase in habitat diversification and/or resource quantity (large scale of effect, *habitat-amount hypothesis*).

Firstly, we started with a state of the art through a literature review in chapter 2 focusing on the importance of disturbance legacies for post-disturbance arthropod communities. In the part II, we studied the specific consequences of forest dieback on habitat (Fig. 1.1), (i) at the European scale with dead wood

(chapter 3) and (ii) in two particular contexts with dead wood and tree-related microhabitats (chapter 4). In addition, there is currently a lack of knowledge regarding the specific effects of habitat changes due to dieback, on biodiversity. We explored this question in the part III, specifically on the response of saproxylic beetles (Fig. 1.1). In the chapter 5, we studied the taxonomic α -diversity and functional traits with a rather local approach while in the chapter 6, we studied both taxonomic and functional α and β -diversities with a rather landscape approach (i.e. through β -diversity). This rather landscape approach in chapter 6 makes the link with the part IV and the chapter 7 that specifically studied the spatial scale of dieback on taxonomic, functional and phylogenetic α -diversity of saproxylic beetles. In addition, we made a literature review in french in the part V, chapter 8 concerning the cascading effects of post-disturbance salvage and sanitation logging on biodiversity and other resilience constituents of forest ecosystem (Fig. 1.1). Finally, we synthesised the thesis results in the chapter 9.

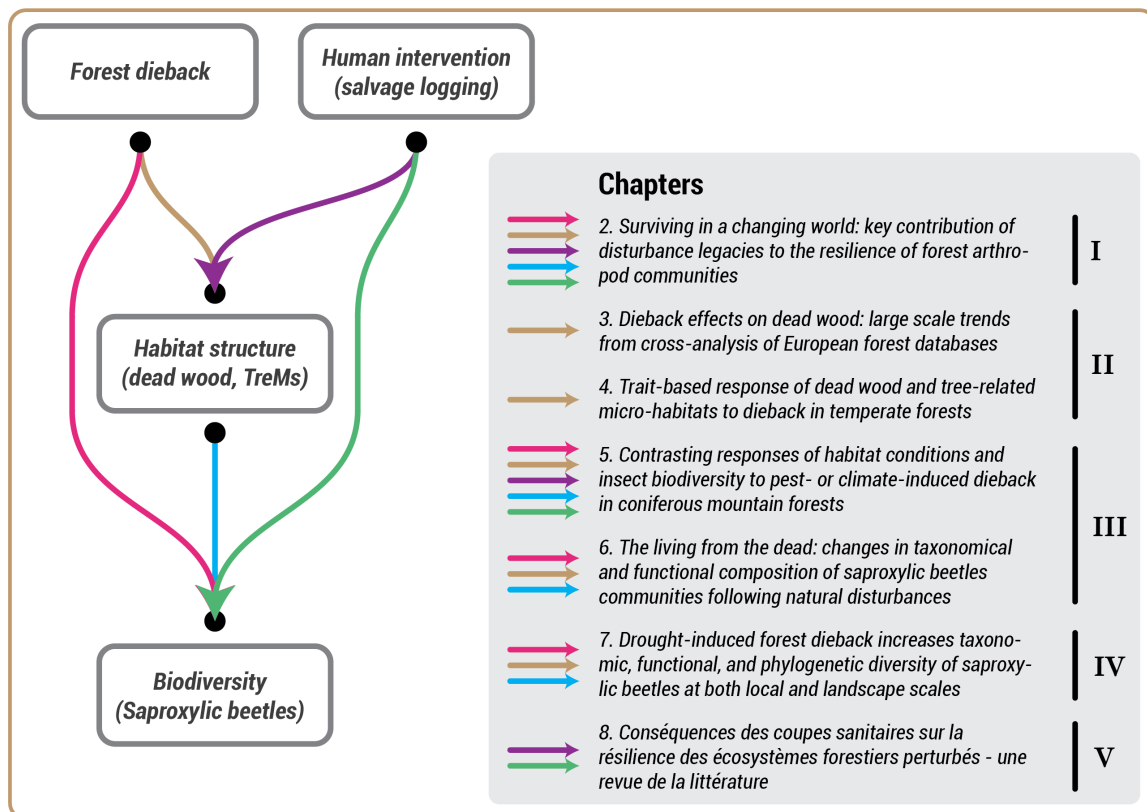










Figure 1.1 – General structure of the thesis in chapters (left in grey area) and parts (right roman numbers in grey area).

Surviving in a changing world: key contribution of disturbance legacies to the resilience of forest arthropod communities

J. COURTS , C. BOUGET , A. LEVERKUS , S. THORN , N. BARSOUM , J. HORÁK , S. PINCEBOURDE , A. SALLÉ 

2.1 Introduction

Major abiotic disturbances in temperate forests worldwide include droughts (Schrader et al., 2004; Senf and Seidl, 2021b; Senf et al., 2018), windstorms (Forzieri et al., 2021; Gardiner et al., 2013; Gregow et al., 2017; Senf and Seidl, 2021c), and wildfires (Dupuy et al., 2020; Forzieri et al., 2021; Senf and Seidl, 2021c). Climate and land-use change have increased the incidence and the ecological consequences of these three disturbances across large areas over the last three decades (Collins et al., 2021; Gregow et al., 2017; Halofsky et al., 2020; McDowell et al., 2020; Seidl et al., 2017; Senf et al., 2020). The frequency, magnitude and intensity (which define the disturbance regime) of droughts, windstorms and wildfires are predicted to increase further in temperate regions with global warming (Samaniego et al., 2018; Seidl et al., 2014b; Spinoni et al., 2018), posing significant challenges to the acclimation and adaptation capacities of temperate forests and their associated communities (Allen et al., 2015; McDowell et al., 2020; Senf and Seidl, 2021b,c; Senf et al., 2018, 2020; Thorn et al., 2019).

Droughts, windstorms and wildfires alter forest ecosystems in several ways, including the availability of water and nutrients (Franklin et al., 2000; Kopáček et al., 2020; Seidl et al., 2016), and the forest microclimate (De Frenne et al., 2021; Thom et al., 2020). Consequently, the physical characteristics of forests are altered, as are key biotic elements such as the distribution and architecture of surviving trees and shrubs, the quantity and viability of their propagules, decomposer and tree symbiont communities (Franklin et al., 2000; Malmström, 2012; Swanson et al., 2011). This has cascading effects on a whole host of forest features such as soil and litter conditions, canopy and understory cover and the availability and distribution of microhabitats (Part II; Franklin et al., 2000; Jørgiste et al., 2017; Kopáček et al., 2020; Sallé et al., 2021; Swanson et al., 2011). Biodiversity can also undergo significant changes, although we still have a poor understanding of how natural disturbances affect temperate forest communities (Thom and Seidl, 2016; Viljur et al., 2022).

Arthropods compose most of the biodiversity on Earth. As such, arthropod communities are a

relevant component of forest biodiversity, worthy of consideration to better understand and predict the consequences of droughts, windstorms and wildfires on forest biodiversity and ecosystem functioning. Arthropods are: (i) a major component of forest biodiversity across multiple strata (i.e. canopy, sub-canopy, forest floor and in soils; Reaka-Kudla et al., 1997), (ii) an important food source for forest-associated species and vital components of complex trophic webs, (iii) key contributors to vital forest ecosystem functions (i.e. pollination, decomposition, biological control of pests and diseases), and (iv) hyper-diverse, displaying significant variation in traits that are reflected in wide-ranging levels of susceptibility to the direct and indirect effects of disturbances (e.g., Dell et al., 2017; Evans, 2005). In addition, they can (v) generate significant disturbance feedback effects (e.g., outbreaks of opportunistic pests; Seidl et al., 2017) and (vi) show rapid responses to disturbance-mediated change.

Understanding the responses of forest arthropod communities to droughts, windstorms and wildfires, and to changes in the regimes of these abiotic disturbances, is necessary in order to anticipate resultant arthropod-associated modifications to forest ecosystem structures and processes, and to identify management options that may be needed to curb negative secondary drivers of forest change stemming from arthropod response to disturbances. An improved understanding is also needed to promote arthropod conservation considering that arthropods are currently in global decline (Cardoso et al., 2020; Hallmann et al., 2017; Lister and Garcia, 2018; Seibold et al., 2019). We currently lack a comprehensive overview of the responses of arthropod communities to key abiotic disturbances in temperate forests. Nonetheless, there is scope to fill this gap and gain significant insights by considering responses of arthropod communities through the lens of disturbance legacies.

Disturbance legacies can be defined as the post-disturbance physical and biological state of an ecosystem. An example of a disturbance legacy is a physical shelter created during a windstorm or a fire which serves to protect organisms and their propagules from the harmful effects of subsequent disturbances (Marzano et al., 2013; Mayer et al., 2022; Swanson et al., 2011). Disturbance legacies also influence the amount, availability and diversity of resources and microhabitats left behind for surviving arthropods following a disturbance (e.g., Cours et al., 2021, 2022; Sallé et al., 2021; Thorn et al., 2014, 2017, 2020). They are consequently key filters that dictate how arthropod communities are shaped as they transition from pre-disturbance to post-disturbance communities (Franklin et al., 2000; Pulsford et al., 2016; Swanson et al., 2011).

Several factors can modulate the nature, amount and spatiotemporal distribution of disturbance legacies, and ultimately the effects they have on the composition and structure of post-disturbance arthropod communities. A prominent factor is the disturbance regime as it dramatically affects the amount, distribution and diversity of disturbance legacies (Chang et al., 2019; Cours et al., 2021; Johnstone et al., 2016; Krawchuk et al., 2020; Pulsford et al., 2016). Other factors include pre-disturbance forest characteristics (i.e. forest stage of development, tree species taxonomic, functional and phylogenetic diversity), which are themselves influenced by forest management strategies and pre-existing disturbance legacies (Fig. 2.1) (Johnstone et al., 2016; Krawchuk et al., 2020; Levine et al., 2022; Lindenmayer et al., 2022; Turner et al., 1999). Intrinsic traits of forest arthropod communities (Fig. 2.1) can also modulate their ability to tolerate disturbances and to exploit the resulting legacies (e.g., Boucher et al., 2016; Dell et al., 2017; Evans, 2005; Ulyshen et al., 2010). Finally, post-disturbance management (Fig. 2.1) can markedly modify the amount of remaining disturbance legacies, and consequently the post-disturbance arthropod communities (e.g., Lindenmayer and Ough, 2006; Müller et al., 2010; Thorn et al., 2017, 2018a, 2020; Waldron et al., 2013).

Our primary aim is to highlight the key environmental filtering roles of disturbance legacies originating from droughts, windstorms and wildfires on arthropod communities in temperate forests. We also consider the contribution of various intensities and methods of both pre- and post-disturbance forest management as an additional filter shaping post-disturbance arthropod communities. Our review is organized into four sections. We first introduce key disturbance legacies associated with droughts, windstorms and wildfires

that have a role in shaping forest arthropod communities and explore how disturbance regimes might affect these legacies. Secondly, we aim to establish how pre-disturbance conditions at tree, stand and landscape scales can affect the nature, distribution and diversity of disturbance legacies. In a third section, we seek to identify the main ecological traits of arthropods affecting their interactions with and responses to disturbance legacies. In a final section, we will evaluate how post-disturbance management strategies can exacerbate or alleviate disturbance impacts on arthropod communities for biological conservation purposes. In a concluding discussion section we will identify key knowledge gaps and propose future research directions.

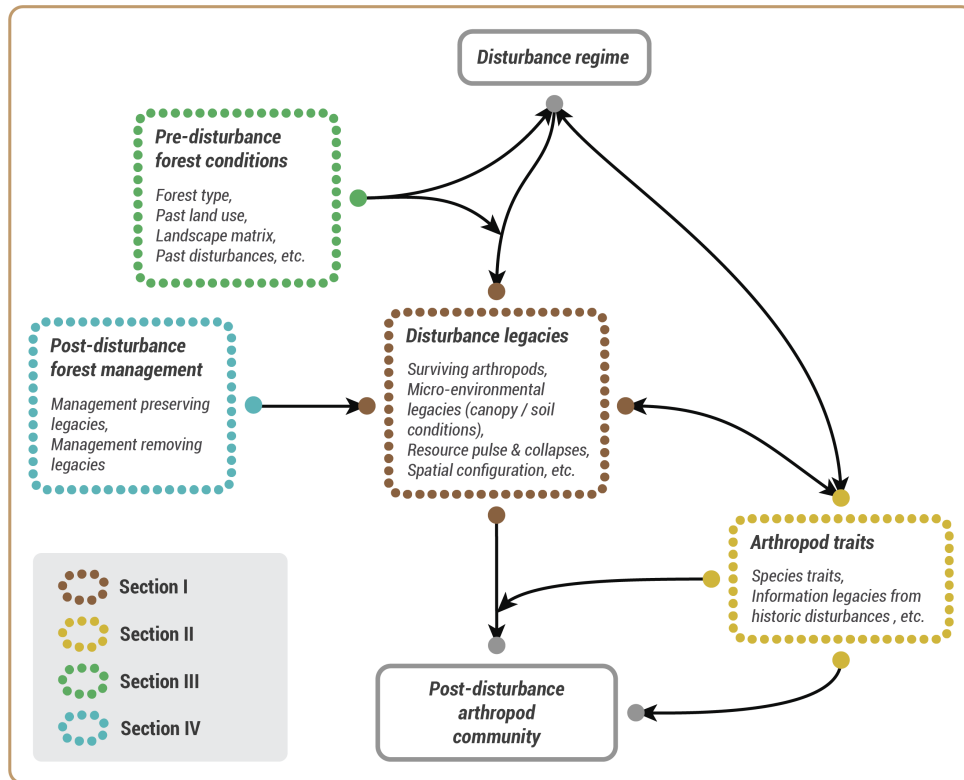


Figure 2.1 – General structure of this review, with factors affecting disturbance legacies and their exploitation by arthropod communities.

2.2 Key legacies of droughts, wildfires and windstorms for arthropod communities

Disturbance legacies are a combination of material and information legacies (Johnstone et al., 2016). Material legacies are the biologically-derived materials left in the wake of disturbances, which include surviving individuals, but also matrices that will provide resources and microhabitats to arthropods (*sensu* Johnstone et al., 2016). Information legacies are ecological traits filtered by the selective pressures exerted by previous disturbances (*sensu* Johnstone et al., 2016).

Droughts, windstorms and wildfires produce some common and idiosyncratic effects on forest ecosystems. Each disturbance can generate a specific set of both material and information legacies for arthropods, further modulated by its regime, pre-disturbance forest condition and ecological traits of arthropod communities (see following sections). Here we describe key disturbance legacies from the point of view of arthropod communities (how arthropod communities respond to legacies, and how arthropod traits modulate their responses, is detailed in section II. These include surviving arthropods,

micro-environmental conditions, and spatiotemporal dynamics of key resources at local and landscape scales.

2.2.1 Surviving arthropods

Large forest disturbances negatively affect populations of many organisms. Wildfires can lead to massive arthropod mortality, and even to local extinctions (Moretti et al., 2006; Wikars and Schimmel, 2001) while windstorms and droughts are less lethal but disturb forest food webs and community structure of above- and belowground arthropod communities (Gely et al., 2020; Jouveau et al., 2022; Lindberg et al., 2002; Peguero et al., 2021; Wehner et al., 2021). Eggs, larvae, pupae, and adult individuals that survive constitute a major disturbance legacy, and their capacity to survive and reproduce in the disturbed landscape sets the basis of the post-disturbance community, until immigration increases (e.g., Brennan et al., 2011; Gongalsky and Persson, 2013; Pryke and Samways, 2012). Surviving arthropods are also key trophic resources for higher trophic levels, including predatory and parasitoid arthropods. Disturbances exert strong selective pressures, promoting information legacies in arthropod communities related to survival and colonization processes (see Sect. 2.3).

2.2.2 Micro-environmental legacies

Microscales are more relevant for most arthropods, due to their small body size (Pincebourde and Woods, 2020). Within forest ecosystems, the canopy and the soil are two key compartments that provide a wide array of resources and microhabitats for the high diversity of forest arthropods (Stork and Grimbacher, 2006). Both compartments can be largely altered by abiotic disturbances. Droughts, wildfires and windstorms can directly affect canopy structure (Bréda et al., 2006; Michaletz and Johnson, 2007; Mitchell, 2013), which is further altered by subsequent tree diebacks and declines (Bär et al., 2019; Beloiu et al., 2022; Ruthrof et al., 2016; Sallé et al., 2021; Senf et al., 2020). This increases canopy openness, which is a major determinant of disturbance-mediated effects on arthropod communities. The reduction of canopy cover considerably disturbs the microclimates from the ground to the upper canopy layer: the higher insolation produces warmer microclimates (e.g., warmer soil surfaces, warmer understory), and a reduced environmental buffer thereby exposing the forest understory to atmospheric temperature extremes (Abd Latif and Blackburn, 2010; Horák et al., 2016; Kopáček et al., 2020; Royer et al., 2010; Zellweger et al., 2020). Furthermore, sun-exposure increases the microclimatic heterogeneity (temperature and humidity) among and within deadwood logs, promoting the species richness of saproxylic beetles at the stand scale (Horák et al., 2016; Lettenmaier et al., 2022; Seibold et al., 2016).

Abiotic disturbances can also have contrasting effects on soil conditions (Coyle et al., 2017). For instance, wildfires remove the litter and some portions of the upper organic horizon (Chanasyk et al., 2003), affect the biochemical properties, alter the texture and reduce the permeability of the soil (Bowd et al., 2019; Certini, 2005; Chanasyk et al., 2003; Nave et al., 2011). Windstorms, on the other hand, generally increase the litter cover and add woody debris (Everham and Brokaw, 1996). The pit-and-mound topography and root plates of uprooted trees in windthrown stands cause small-scale gradients in the soil water contents, temperature and litter accumulation (Bouget and Duelli, 2004), providing refugia from desiccation under canopy gaps (Thorn et al., 2016c; Viljur et al., 2022). Droughts reduce soil water films and increase soil hardness, which could impede the movements of soil fauna (Coyle et al., 2017). Disturbance-driven changes in micro-environmental conditions can in turn impact the development, survival and behaviour of ground- and canopy-dwelling arthropods, and ultimately the composition and structure of their community (Peguero et al., 2021; Perry and Herms, 2019; Perry et al., 2021; Sallé et al., 2021; Véle et al., 2016; Viljur et al., 2022), but see below (Sect. 2.3).

2.2.3 Resource pulses and collapses

Disturbances affect the diversity and the amount of resources for arthropods. In this regard, the timescale of disturbances is important as both amplitude and direction of resource fluctuations can vary depending on the time frame considered (e.g., Barreiro and Díaz-Raviña, 2021; Potts et al., 2003; Tab. 2.1). Some resources may suddenly collapse or increase at the onset of a disturbance (e.g., deadwood after windstorm), but the temporal dynamics may differ considerably among resources.

Some resources can be markedly reduced or locally depleted as a direct consequence of a disturbance. Degraded canopies provide less foliage (Sallé et al., 2021). Flowers and fruits may abort during drought (Fernández-Martínez et al., 2012; Nussbaumer et al., 2020) and, over longer time scales, weakened trees produce less reproductive organs (Gavinet et al., 2019; Tab. 2.1). Nonetheless, large mast events occasionally occur following disturbances (Ascoli et al., 2015; Losseau et al., 2020; Vacchiano et al., 2017, 2021), and may provide a pulse of flowers, fruits and seeds that remain hardly predictable. Abiotic disturbances may also alter the nutritional value of host plant tissues and their content in defensive compounds, which in turn alter their resistance to phytophagous insects (Gely et al., 2020; Huberty and Denno, 2004; Jactel et al., 2012). In this regard, the immediate and short-term effects of drought have been investigated in several tree species, and the outcomes largely depend on drought severity and duration (Gely et al., 2020; Huberty and Denno, 2004; Jactel et al., 2012). Similar modifications probably occur over long-time scales in declining trees, although evidence is lacking (Sallé et al., 2021). Overall, the quantitative and qualitative fluctuations of these canopy-related resources during decline or dieback processes have been poorly documented so far (Ishii et al., 2004; Sallé et al., 2021).

The reduction of canopy cover stimulates successional dynamics and provides colonization opportunities for early successional and thermophilous plant species (Clements, 1916; Dietz et al., 2020; Peterson and Pickett, 1995; Tanner et al., 2022; Thom et al., 2017b; Zellweger et al., 2020). Depending on disturbance type, spatial extent and severity, the change in canopy cover could be important also for late-successional and shade-tolerant species (Chang et al., 2019; Lu et al., 2019; Turner et al., 1997). As a result, windstorms and wildfires may promote plant species richness in the herbaceous layer, but have contrasted effects on plant functional diversity and traits (Burkle et al., 2019; Cacciatori et al., 2022; Day et al., 2020; Lu et al., 2019; Turner et al., 1997), with cascading effects on arthropod communities. More specifically, canopy opening can increase ground-related floral resources available for pollinators (Burkle et al., 2019; Romey et al., 2007), and wildfires improve the amount and diversity of ground-nesting sites for arthropods (Burkle et al., 2019). This is however a rather short-lived resource pulse as few years after disturbance floral resources tend to decrease (Potts et al., 2003). In addition, increased canopy openness accelerates decomposition and could provide a pulse of microbial resources and nutrients for soil arthropods (Perry et al., 2018; Runkle, 1985).

On the ground, wildfires can consume large patches of the litter and superficial organic horizon (Certini, 2005; DeBano et al., 1998), and leave a charred biomass with altered biochemical properties for long periods (Bowd et al., 2019; DeLuca and Aplet, 2008). This can profoundly alter the microhabitats and trophic resources for soil arthropods, but also for other forest arthropods with ground-dwelling life stages (Verble-Pearson, 2014). Soil microorganisms are also a food source for soil-dwelling arthropods (Peguero et al., 2021; Pollierer et al., 2012). The immediate consequences of wildfires on soil microorganisms are a decrease in abundance, biomass and richness, and an alteration of their community structure (Barreiro and Díaz-Raviña, 2021; Pressler et al., 2019). Likewise, drought adversely affects microbial communities in forest soils, at least over short time scales (Bastida et al., 2017; Lindberg et al., 2002; Peguero et al., 2021; Santonja et al., 2017). However, responses of the soil microbial community can also be more complex, positive, negative, or with a different amplitude, when longer periods following the disturbance are considered (Barreiro and Díaz-Raviña, 2021; Liu et al., 2022).

Disturbances may also lead to transient increases of resources which are traditionally scarce in managed

forest ecosystems, and thus, enhance the structural heterogeneity of the ecosystem (Kulakowski et al., 2017; Meigs et al., 2017; Sallé et al., 2021; Schoennagel et al., 2008). One of the best examples is the accumulation and diversification of deadwood resources. Droughts and windstorms promote the accumulation of fallen twigs, branches, stems, uprooted trees and logs on the ground, snags and perched dead branches in the canopy (Cours et al., 2021; Swanson et al., 2011; Thorn et al., 2017). Another important factor driving arthropod communities is tree-related microhabitats (TreMs). Gales, canopy openness and compromised tree health can promote the formation of TreMs like bark scratches, bark cracks, loose bark, mistletoe, and dead branches (Kozák et al., 2021; Larrieu et al., 2022; Ojeda et al., 2007). Snags also offer more TreMs than living trees (Asbeck et al., 2022; Paillet et al., 2017). As a result, disturbances can significantly affect the assemblages of TreMs (Sect. 4), thereby generating legacies that could have positive consequences for arthropod species associated with these resources (see below). Disturbances may also occasionally generate very particular substrates and environmental conditions, thereby promoting peculiar arthropod communities. For instance, wildfires can produce large amounts of sun-exposed charred deadwood, yielding to specific communities of "burn-associated" saproxylic beetles (Boucher et al., 2012, 2016). Following disturbances, fallen and weakened trees also constitute a major pulse of suitable breeding substrates for opportunistic pest species (Kausrud et al., 2012; Korolyova et al., 2022; Paine et al., 1998; Rouault et al., 2006; Sallé et al., 2014).

Together with contrasting survival among species, and micro-environmental legacies, resource pulses and collapses contribute to the structural complexity of forest ecosystems over several spatial and temporal scales (Ishii et al., 2004; Krawchuk et al., 2020; Meigs et al., 2017; Schoennagel et al., 2008). This increases the variability of available niches at different ecological scales, changes interspecific interactions, creates colonization opportunities for novel species and can be major drivers of post-disturbance community structure for arthropods (Horák, 2021; Ishii et al., 2004; Pulsford et al., 2016).

2.2.4 Composition, organisation and spatial patterns of disturbance refugia

Forest patches that are less affected by disturbances are called disturbance refugia (Camp et al., 1997; Krawchuk et al., 2020). Depending on the disturbance regime, disturbance refugia can be comparable to unaffected islands within a disturbed landscape matrix, but they can also be more diffuse and less clearly delineated (Krawchuk et al., 2020; Meddens et al., 2018). These refugia constitute reservoirs of genetic diversity and propagules from pre-disturbance communities, from which recolonization of disturbed areas can take place (Krawchuk et al., 2020; Meddens et al., 2018; Seidl et al., 2014a). They can also provide resources, suitable microhabitats and micro-environments in an otherwise hostile environment for survivors of the disturbance (Krawchuk et al., 2020; Meddens et al., 2018). In this regard, the spatial pattern of disturbance refugia can be a key driver of forest ecosystem resilience. The size and distribution of disturbance legacies will affect whether post-disturbance arthropod communities will be a result of recolonization processes, or derive from survivors. Disturbance refugia also contribute to the spatial heterogeneity at the landscape scale, especially if refugia and the disturbed landscape matrix follow different recovery pathways (Meddens et al., 2018).

Table 2.1 – *Effects of drought over immediate, short-termed and delayed time scales on trophic resources and microhabitats.*

Habitat - Resource	Drought effects		
	Immediate	Short term (1 year)	Delayed (several years)*
Tree-related microhabitats	Null/Positive: cavitation can generate dry branches.	Positive: partial branch mortality triggers an accumulation of dead wood in the canopy. Tree mortality can occur if the water constraint was severe and the resulting snags can accumulate diverse TreMs.	Positive: drought legacy effects can lag for several years and induce progressive tree decline and mortality resulting in a progressive accumulation of TreMs in the canopy and on the trunk (dead branches, loose bark and bark cracks, cavities, etc.).
Foliage	Negative: premature leaf shedding occurs during severe droughts to reduce the drying rate.	Positive / negative in the herbaceous / shrub layer: increased canopy openness can favor the vegetation but this can also lead to harsher environmental conditions. Negative in the canopy layer: (i) partial branch death reduces foliage abundance; (ii) decreased C allocations to non-perennial organs reduce the amount of buds and foliage.	Positive / negative in the herbaceous / shrub layer: increased light and precipitation can favor vegetation but increased canopy openness can lead to harsher environmental conditions. Negative / null in the canopy layer: (i) gradual increase in dead branches progressively reduces foliage abundance and lead to increased canopy openness; (ii) decreased C allocations to non-perennial organs reduce the amount of buds and foliage. Resilient trees may compensate crown degradation with epicormic shoots.
Fruits and seeds	Null / negative: premature abscission or fruit abortion can occur during severe summer droughts.	Null / positive in the canopy layer: large mast events can occur following droughts. Positive in the herbaceous / shrub layer: increased canopy openness can promote floral resources.	Positive in the herbaceous / shrub layer: increased canopy openness can promote floral resources. Negative in the canopy layer: (i) reduced amount of branches reduces the amount of reproductive structures; (ii) carbon allocation to perennial organs reduces the size and abundance of reproductive organs.

*variable according to stand resilience.

Here it is considered that the expected repeated droughts will compromise tree recovery

2.2.5 Disturbance regimes and disturbance legacies

Disturbance regimes define the type, amount and diversity of legacies that commonly occur in an ecosystem. For instance, the intensity and severity of a disturbance drive its impacts on the amount of surviving arthropods, the amplitude of deadwood resources pulses, the impact on soil condition, and the size of canopy gaps (e.g., Bento-Gonçalves et al., 2012; Smirnova et al., 2008; Verble-Pearson, 2014). Disturbance frequency affects information legacies. Recurrent disturbances leave evolutionary imprints on communities, as for pyrophilous plants and arthropods in fire-prone ecosystems (Evans, 2005; Keeley et al., 2011; Pausas et al., 2004, 2008), and may consequently increase ecosystem resilience and resistance capacities to subsequent disturbances (Seidl et al., 2014a). The spatial extent of disturbances influences micro-environmental conditions at local scales, and the spatial distribution of refugia in the landscape (Turner, 2010).

Through legacies, successive disturbances can interact and have antagonistic, synergistic or additive effects (e.g., Kulakowski and Veblen, 2002; Littell et al., 2016; Seidl and Rammer, 2017; Seidl et al., 2017). In this context, legacies from one disturbance can modify ecosystem resistance and resilience to a second disturbance (Buma, 2015; Cannon et al., 2017; Paine et al., 1998; Simard et al., 2011). For example, the pulse of deadwood and litter resources on the ground following a windstorm can promote the spread of subsequent wildfires (Donato et al., 2006; Myers and van Lear, 1998). Likewise, windstorms

may reduce mature tree density and seed availability, and consequently delay the recovery following a wildfire (Buma and Wessman, 2011). Successive disturbance events can also generate peculiar legacies. For example, disturbance legacies of reburned forests are composed of lesser deadwood amounts, with altered physical and biochemical characteristics, compared to forests burned only once (Donato et al., 2016).

2.3 Forest arthropod responses to disturbance legacies

2.3.1 Critical traits of arthropod communities affecting their responses to disturbances

Responses to disturbance can be grouped into general strategies according to the life-history traits allowing population recovery and persistence despite (or because of) disturbance (Rowe, 1983): (i) *invaders* are opportunistic species, taking advantage of disturbance legacies and colonizing recently disturbed areas; (ii) *evaders* rely on specialized strategies to “get around” the disturbance, being able to immediately reestablish post-disturbance populations; (iii) *resisters* strive to survive the disturbance itself, using specialized mechanisms to withstand direct disturbance-induced mortality or to recover after the disturbance event (e.g., survivors, see Sect. 2.2.1); (iv) *avoiders* are not considered disturbance-adapted, and are only found in late successional stages. In this section we review the traits and strategies by which the four categories of organisms (i) increase their survival to the disturbance, (ii) re-colonize and/or exploit spatial refugia, (iii) exploit the novel micro-environmental legacies associated with the disturbance, and (iv) make use of the pulse and collapse of resources.

Traits related to survival to direct effects of abiotic disturbances

Many “resisters” have at least one of their life stage occupying micro-environment that could act as refugia such as belowground (e.g., Dell et al., 2017), within plant tissues or plant shelters (e.g., Brennan et al., 2011; Morelli et al., 2020; Romero et al., 2022; Suggitt et al., 2018; Ulyshen et al., 2010), or in patches that remain unaffected by the disturbance (Krawchuk et al., 2020). For instance, arthropods that have the capacity to use deeper portions of the soil profile have better chances to survive the burn or to avoid the impacts of desiccation (Coyle et al., 2017; Jue et al., 2022; Mason et al., 2021; Pryke and Samways, 2012; Radea and Arianoutsou, 2012). Likewise, burrowing spiders, ground- and deadwood nesting bees and ants, and larvae of saproxylic beetles within large-diameter logs can survive to heat and direct flames from ongoing fires (Caut et al., 2014; Graham et al., 2009; Kwon et al., 2013; Langlands et al., 2011; Mason et al., 2021; Simmons and Bossart, 2020; Ulyshen et al., 2010; Verble-Pearson, 2014). The overlap between disturbance seasonality and arthropod phenology influence the likelihood of negative effects. For instance, in Mediterranean ecosystems, summer wildfires have a lower impact on soil arthropods as most of them migrate into deeper soil layers or enter a cryptozoic stage at that time of year (Henig-Sever et al., 2001).

Some morphological traits also contribute to disturbance resistance. Drought-resistant species are equipped with specific protective body traits like hairs and thick cuticles (Coyle et al., 2017; Langlands et al., 2011), and exhibit a physiological xerotolerance (Thorn et al., 2016c; Urbanovičová et al., 2014). Thick cuticles enhance resistance to wildfires (Wikars and Schimmel, 2001), and small arthropods (e.g., Acari) tend to be more sensitive to changes in soil temperature and dryness than larger organisms (e.g., Collembola) (Bokhorst et al., 2012; Buckingham et al., 2019; Moretti et al., 2006).

Several “evaders” are able to detect wildfires well in advance, using olfactory or auditory cues, and may rapidly engage in escape behaviors and actively flee to disturbance refugia (Dell et al., 2017; Moretti et al., 2006). In this regard, high mobility is a key asset to avoid deleterious disturbance effects. Winged insect orders have consequently higher survivorship to wildfires than less-mobile taxa (Dell et al., 2017), and smaller-bodied soil fauna have a higher ability to shelter from wildfires and move to refugia

like underground burrows, below rocks, or within trunks or roots (Coyle et al., 2017). Above-ground arthropods may also escape from wildfires by actively burrowing into the soil, or by moving upward into the cooler canopy during low-intensity surface wildfires (Dell et al., 2017; Pausas and Parr, 2018).

Vulnerability of organisms to abiotic disturbances depends on their preferred microhabitat (Brennan et al., 2011), especially across the vertical gradient of forests. Ferrenberg et al. (2006) suggested that aboveground communities experienced relatively greater influences of deterministic processes, while the relative influence of stochastic processes increased for belowground communities. Canopy arthropods may be spared by surface fires, and they may be more severely exposed to heatwaves (Sallé et al., 2021). Epigeic organisms that live in the upper soil layers are also likely to experience stronger disturbance-induced fluctuations in temperature and moisture compared to their deeper-dwelling counterparts (Coyle et al., 2017).

Traits related to post-disturbance colonization processes and spatial patterns of disturbance refugia

Colonization and re-colonization processes depend on the proportion of arthropods that survived in situ or in distant disturbance refugia. Post-disturbance arthropod communities can be dominated at first by disturbance-adapted taxa, as observed following wildfires (Pryke and Samways, 2012). "Invaders" can also rapidly colonize disturbed areas. This colonization of new habitat patches or newly-created substrates entails the ability of these arthropods to detect material legacies. Phytophagous arthropods can detect weakened or freshly dead trees through emission of kairomones like ethanol (e.g., Miller and Rabaglia, 2009). Pyrophilous insects, seeking burnt substrates, possess specialized chemoreceptors that sense smoke volatiles, and/or sensilla that respond to radiant heat and infrared (Evans, 2005; Pausas and Parr, 2018). It seems that overall saproxylic beetles have also particular sensor to trace dead wood through landscape Graf et al. (2022).

Response to disturbances also selects traits related to mobility (Moretti and Legg, 2009). "Invaders" are by definition highly mobile, as they exploit ephemeral resources in post-disturbance environments (Percel et al., 2019; Saint-Germain et al., 2013). Similar traits are also selected in "evaders" and "avoiders", especially when disturbance refugia are highly scattered throughout the landscape. The composition of post-disturbance communities highlights the importance of dispersal events in disturbed areas. For example, windthrown and burnt areas hosted lower numbers of brachypterous ground beetle species, but higher numbers of macropterous species than undisturbed forests (Bouget, 2005b; Samu et al., 2010; Sklodowski and Garbalinska, 2011). Similarly, the abundance of spiders with greater ballooning dispersal ability (Langlands et al., 2011) and of wild bees with a high dispersal capacity increased in recently burnt sites (Mason et al., 2021). As a result, the functional spatial scale depicting the effect of windstorms on arthropod communities increases with their dispersal capacity (Hirao et al., 2008). In addition, as body size is related to dispersal ability, the community dominance in post-disturbance soil communities may shift from small-bodied to relatively larger-bodied individuals (Bokhorst et al., 2012; Buckingham et al., 2019).

The colonization of material legacies also involves demographic parameters, and the best "invaders" should have short generation times, a high fecundity and long life spans. For instance, eusocial bees, which are active across seasons and have several generations per year, can quickly rebound following a fire during the early growing season (Simmons and Bossart, 2020). Similarly, their large brood production, their small body size, and their diverse food niches and relatively broad diets allow ants to rapidly recover after wildfires and keep nearly stable populations (Bess et al., 2002). These demographic parameters might be particularly relevant for recolonization processes when disturbance refugia are small compared to the surrounding disturbed matrix and consequently shelter a small reservoir of "avoiders" and "evaders".

In addition to the availability of space and new trophic resources, the local extinction of certain taxa may constitute an opportunity for the immigration of exotic invasive species in disturbed patches.

In line with this hypothesis, *Cacyreus marshalli*, an invasive butterfly, appeared in a Mediterranean shrubland after a wildfire (Scandurra et al., 2014), and frequent wildfires increased the likelihood of exotic ant species establishment in pine forests (Atchison et al., 2018). Likewise, arthropods can also take advantage of post-disturbance conditions because of potential reductions in predation (Pausas and Parr, 2018) or competition pressures (Radea and Arianoutsou, 2012). *Tentyria grossa*, a rare soil species, became dominant after wildfires in Italy partly because of the decreased abundance of almost all other related species (Fattorini, 2010). Likewise, resources created by large disturbances in Central Europe led to the return of *Peltis grossa*, a primeval forest specialist (Busse et al., 2022).

Traits related to micro-environmental legacies

In general, stand-replacing disturbances benefit taxa that are adapted to more open conditions (e.g., open-land ground-dwelling carabids, ground hunting spiders or some saproxylic beetles), while groups typically associated with shady conditions (e.g., forest-preferring ground-dwelling carabids, sheet-web weaver spiders, and shade-preferring saproxylophagous species) are negatively impacted (Bouget, 2005a,b; Černecká et al., 2020; Horák et al., 2016; Lettenmaier et al., 2022; Rodrigo et al., 2008; Seibold et al., 2016).

Disturbances also disrupt humidity patterns. Post-fire environments have drier atmospheric and soil conditions. These environmental conditions shifts the composition of arthropod communities towards a dominance of drought-resistant species (Coyle et al., 2017; Langlands et al., 2011), while hygrophilous taxa are negatively affected (Samu et al., 2010; Sklodowski and Garbalinska, 2011; Thorn et al., 2016c).

Open conditions also imply exposure to predators for arthropods (Černecká et al., 2020; Košulič et al., 2016). Consequently, for some arthropod taxa the frequency of dark cryptic individuals increases in burned areas (Pausas and Parr, 2018). Camouflage abilities may be favored in disturbed forests but we lack knowledge on this topic.

Traits related to responses to resource pulses and collapses

Disturbance legacies generate pulses or collapses of critical resources for arthropods. Larger impacts on arthropod communities are expected shortly after the disturbance initiates, but changes in community structure may last beyond a decade (Georgiev et al., 2022). The responses of arthropod communities to these changes in resources diversity, amount and accessibility is largely mediated by their ecological / trophic guilds.

In response to abundance and diversity pulses in deadwood substrates and associated TreMs, higher diversity and abundance of deadwood-associated arthropods are commonly observed in disturbed stands (Viljur et al., 2022). This also affects the taxonomic, functional, and phylogenetic composition of species in disturbed forests (Cours et al., 2022; Kozák et al., 2021; Sire et al., 2022). Saproxylic insects, in general, benefit from these pulses (Beudert et al., 2015; Cours et al., 2021, 2022; Thom and Seidl, 2016; Thorn et al., 2016c, 2017; Viljur et al., 2022), including saproxylophagous arthropods (Ferrenberg et al., 2006), cavity-nesting species (Simanonok and Burkle, 2019), and xylomycetophagous and mycophagous insects (Bouget, 2005a; Cours et al., 2022; Wikars, 2002), unless wildfire has altered wood biochemical properties (Tello et al., 2020).

The pulse of weakened host trees following severe forest disturbances also promotes xylophagous species, and may trigger outbreaks of opportunistic pests (Sect. 2.4.2). The impacts of tree dieback or decline on crown-related resources has more contrasted effects on leaf-dwelling guilds. Overall it negatively affects specialized leaf-feeders, but has no effect on seed and fruit consuming species, for which responses to variations in food are generally poorly informed (Sallé et al., 2020).

The pulse of the herbaceous layer vegetation and floral resources, related to increased canopy openness, consistently promoted understory-associated herbivores and pollinators (Viljur et al., 2022). This may

also favor insects with rhizophagous larvae. Regrowth of above ground vegetation immediately after destruction and post-fire increased habitat heterogeneity have also been found to lead to greater abundance of herbivores in the mid-term (Thompson et al., 2022a).

Belowground, soil arthropods exhibit an overall negative short-term response to wildfires, as a consequence of collapses in microbial resources (Kwon et al., 2013), and detrimental soil conditions (Hartshorn, 2021; Kwon et al., 2013; Radea and Arianoutsou, 2012). Their response to wildfire and similar disturbances is often strongly determined by the depth of remaining litter (Ferrenberg et al., 2006; Iida et al., 2021; Verble-Pearson, 2014). The response may be different following windstorms or later during the ecosystem recovery process, as post-disturbance conditions may promote some guilds of soils arthropods (Čuchta et al., 2013; Hartshorn, 2021; Urbanovičová et al., 2014). They may benefit from the pulse of easily-decomposable organic matter from damaged plants, and from the related pulse in microbial activity (Perry et al., 2018), but also from changes in micro-environmental conditions related to canopy opening (Perry et al., 2018), although this latter point is debated or may depend on the taxonomic groups or functional guilds considered (Čuchta et al., 2013; Sterzyńska et al., 2020). In addition they may benefit from the mosaic of soil microhabitats created by abiotic disturbances, especially windstorms (Bouget and Duelli, 2004; Viljur et al., 2022).

Populations of predatory arthropods may be driven by disturbance-induced variations in prey availability. Surviving predators may benefit from surviving prey and an increase in deadwood- and litter-dwelling prey (Underwood and Quinn, 2010). Conversely, the general decrease in detritivores may have cascading effects on higher trophic levels as suggested by reductions in surface predators, such as spiders, centipedes, and predatory ground beetles (Bouget and Duelli, 2004; Coyle et al., 2017; but see Černecká et al., 2020; Košulič et al., 2016). Nonetheless, we compiled inconsistent bottom-up effects on higher trophic levels in saproxylic (Cours et al., 2021; Vincent et al., 2020) and soil food webs (Delph et al., 2014). This means that predaceous groups can both increase or decrease in disturbed stands compared with undisturbed forests, and the drivers of the direction of the effects remains to be better understood.

Spatiotemporal changes in community structure

The increase in within-patch heterogeneity in disturbed areas may play an important role in community organization by niche partitioning among species (Bouget and Duelli, 2004). Post-disturbance conditions may result in an increased range of food sources and breeding substrates for some guilds of arthropods, expanding their trophic and reproductive niche space and resulting in a potential functional divergence in the disturbed area (Lettenmaier et al., 2022; Moretti et al., 2010). At the same time, micro-environmental legacies could lead to functional convergence and decrease in trait variations, by reducing abiotic niche space and selecting species with narrow microclimatic requirements, i.e. xerothermic, heliophilous, diurnal species (Moretti et al., 2010).

Community patterns actually hinge on spatiotemporal post-disturbance dynamics, depending on both the time elapsed since disturbance and the surrounding landscape composition. Environmental effects of disturbance on forest arthropod communities depend on microhabitat and resource patch dynamics, on accumulation and depletion patterns, and can be ephemeral or long-lasting, immediate or delayed, or even time-cumulative. Saproxylic insect assemblages associated with older burned forests consist in a mix of pyrophilous specialists and non-pyrophilous secondary users, i.e. opportunistic generalist saproxylic species which are not restricted to freshly fire-killed wood but which benefit with delay from fire-induced deadwood pulses (Saint-Germain et al., 2013). Community dynamics of ground-dwelling arthropods in windthrown areas are also a matter of time since disturbance, with positive effects of short-term pulses of litter after windstorm, and then mid-term depletion of litter after the decrease in leaf area on weakened trees (Coyle et al., 2017).

Environmental effects of disturbance acting on local arthropod communities may arise from local or

large-scale patterns of disturbance. In silver fir Pyrenean forests, the local abundance of wood-eating species was positively affected by local forest dieback only if the landscape dieback level was high (Cours et al., 2022), in agreement with the habitat amount hypothesis (Fahrig, 2013; Seibold et al., 2017). Nonetheless, the local abundance of pioneer xylophagous beetle species did not correlate with increasing windstorm gap area in a severely disturbed landscape (Bouget, 2005a). In line with the resource concentration hypothesis and mass effects, flower-visiting saproxylic beetles were more abundant in mid-size and large windthrow gaps than in small ones (Bouget, 2005a).

2.3.2 Interactions among disturbance legacies, insect outbreaks and arthropod communities

The pulse of weakened host trees following severe abiotic disturbances may promote outbreaks of opportunistic bark and wood-boring insects, bark beetles being a paramount example, which are major biotic disturbances causing forest diebacks sometimes over large spatial extents (Bentz et al., 2010; Biedermann and Vega, 2020; Kausrud et al., 2012; Korolyova et al., 2022; Paine et al., 1998; Rouault et al., 2006; Sallé et al., 2014). These opportunistic insects can also act as aggravating factors of multifactorial forest declines, further deteriorating stand conditions in previously disturbed areas (Sallé et al., 2014). Severe droughts and windstorms are major drivers of such outbreaks (Bentz et al., 2010; Biedermann and Vega, 2020; Pineau et al., 2017; Sallé et al., 2014). Since wildfires may have deleterious effects on breeding substrates (Kulakowski et al., 2012), they only occasionally contribute to large-scale outbreaks (Breece et al., 2008; Carter et al., 2022; Jenkins et al., 2014; Lombardero and Ayres, 2011; Powell et al., 2012; Tabacaru et al., 2016).

Compound disturbances can lead to a situation when a disturbance alters ecosystem response to a subsequent disturbance (Sect. 2.2; Paine et al., 1998). Large-scale outbreaks of opportunistic pests trigger or contribute to extended forest diebacks and declines (Bentz et al., 2010; Biedermann and Vega, 2020; Pineau et al., 2017; Sallé et al., 2014), and have consequently compounded effects with wildfires, windstorms and drought since they contribute to increase the severity and spatial extent of their impacts on forest ecosystems (Lloret and Kitzberger, 2018; Pile et al., 2019). Consequently, they amplify some disturbance legacies of previous disturbances like the amount of deadwood, TreMs, and canopy openness (Beudert et al., 2015; Cours et al., 2021). Cascading effects on arthropod communities are consequently similar to those of abiotic disturbances: flower-visiting insects (Beudert et al., 2015; Cours et al., 2021; Kortmann et al., 2022; Lehnert et al., 2013; Thom et al., 2017a) are stimulated in canopy gaps as a result of micro-environmental legacies and related pulses of plant resources (Burkle et al., 2019; Davis et al., 2020). Conversely, taxonomic groups linked to closed-canopy forests, such as Mycetophilidae, might suffer from canopy opening and the desiccation of decaying litter (Lehnert et al., 2013). Increase in deadwood volume, in sunnier environments, fosters the diversity of saproxylic beetles (Beudert et al., 2015; Horák et al., 2016; Lettenmaier et al., 2022; Seibold et al., 2016), although the trend varies with the dynamics of dieback (Cours et al., 2021). However, several soil-dwelling groups (ground beetles, harvestmen, springtails) seem to be unaffected in bark beetle infestation spots (Beudert et al., 2015; Winter et al., 2015) compared with undisturbed forests. The response of fungus-dwelling arthropods to bark beetle-induced diebacks depends on inconsistent variations in wood-inhabiting fungi (Beudert et al., 2015; Cours et al., 2021), and on the profound decrease in biomass of the forest soil fungus community, reflecting both the disappearance of fungi symbiotic with tree roots and the changing availability of needle litter (Štursová et al., 2014). Overall, eruptive pests, like the spruce bark beetle in Europe, may be considered as a keystone ecosystem engineer, providing habitat structures that promote the occurrence of endangered species (Busse et al., 2022; Cours et al., 2021; Hilszczański et al., 2016; Mikoláš et al., 2017; Müller et al., 2008).

Outbreaks of opportunistic pests are triggered by abiotic disturbances, but through their disturbance legacies, they can also have in turn additive or synergistic effects on these abiotic disturbances (Seidl

et al., 2017). For instance, fuel accumulation following outbreaks may promote subsequent wildfires, depending on time since outbreaks, and fuels and fire characteristics (Carter et al., 2022; Harvey et al., 2014; Hicke et al., 2012, but see Meigs et al., 2016; Simard et al., 2011). Likewise, increased canopy openness may amplify the impact of subsequent droughts on forest stands (Koelemeijer et al., 2022; Littell et al., 2016), and similar effects could be expected following large-scale outbreaks. Outbreaks may also have compounded effects with wildfires as, depending on disturbance severity and forest type, they may alter recovery processes following a subsequent wildfire (Carlson et al., 2017; Kleinman et al., 2019; Schapira et al., 2021).

2.4 Pre-disturbance forest conditions: from forest traits to long-term legacies

2.4.1 Pre-disturbance forest type

Pre-disturbance vegetation

Initial stand characteristics modulate the composition of post-disturbance vegetation (Johnstone et al., 2010; Turner et al., 1999). For instance, the maintenance of trees and understory seedlings and saplings after a disturbance significantly contribute to the vegetation composition after disturbance (DeRose and Long, 2010; Frelich and Reich, 1999; Reyes and Kneeshaw, 2008; Webb and Scanga, 2001). Depending on the degree of reorganization undergone by pre-disturbance vegetation, and disturbance type, forest ecosystems could then follow different pathways leading to resilience (i.e. no change in structure and composition), restructuring (i.e. structure changes but not composition), reassembly (i.e. composition changes but not structure), or replacement (i.e. both structure and composition change; Seidl and Turner, 2022). While forest resilience may also promote the resilience of forest arthropod communities, the three other pathways should reshape arthropod communities to varying extents. In this regard, Iida et al. (2021) found that, following a volcanic eruption, pre-eruptive vegetation influenced post-disturbance communities of ground-dwelling arthropods. Nonetheless, this effect was strongly mediated by disturbance severity and/or type, and by the depth of remaining litter.

At the species and individual levels, several characteristics can affect tree resistance to drought, wind-storm or wildfire, and there is a large interspecific variation in tree susceptibility to these disturbances (e.g., Canham et al., 2001 for windstorms; Choat et al., 2018 for droughts; Bär et al., 2019 for wildfires). For instance, large trees are generally more resistant to fire damage (Charnley et al., 2017; Turner et al., 1999). Several of these traits are information legacies, selected by former historical disturbances. Pyrophytic species with specific traits like serotiny, thick bark, high resprouting capacities, and lignotubers, providing resistance and resilience to wildfires, are examples (Collins et al., 2019; Gauthier et al., 1996; Keeley et al., 2011). These information legacies can be paramount drivers of ecosystem resilience (Bowd et al., 2021c) as they modulate the nature and spatial pattern of disturbance refugia on scales ranging from the tree to the landscape (Krawchuk et al., 2020). Resistant trees can act as disturbance refugia for arthropod communities since they allow the persistence of suitable micro-environmental conditions and trophic resources for arthropod communities during the disturbance, and in post-disturbance conditions. For instance, the fire-resistant grass trees in Australia have tightly packed leaves around their apical stem, which provide micro-climatic refugia for several arthropod taxa and allow recolonization processes following wildfires (Brennan et al., 2011). Crawling arthropods also climb into the canopy to escape from surface fires (Dell et al., 2017).

Conversely, some characteristics of disturbance-adapted tree species may also increase the intensity, severity or spatial extent of disturbances. For instance, leaf moisture content, leaf area and leaf chemistry affect the flammability of trees and influence wildfire spread within stands (Popović et al., 2021), and

at landscape scales (Carlson et al., 2011). Highly flammable tree species may also provide disturbance refugia for arthropods (e.g., Brennan et al., 2011), but forests dominated by such tree species should promote disturbance-prone arthropod communities, and communities associated with open habitats.

Tree characteristics also influence key resource pulses. For instance, there is a significant interspecific variability in decomposition rates of deadwood (Harmon et al., 2020; Kahl et al., 2017). This affects the amount, diversity and persistence of deadwood resources, and modulates post-disturbance communities of saproxylic arthropods (Seibold et al., 2022). Tree species, and some morphological features like trunk diameter, also significantly influence the ontogenesis, and ultimately the assemblages of TreMs (Courbaud et al., 2022; Larrieu et al., 2022; Paillet et al., 2019). Interestingly, early-successional species promoted by stand-replacing disturbances, develop different TreMs than mid- and late-successional species promoted by low- and mid-severity disturbances (Courbaud et al., 2022; Kuuluvainen, 2016). Therefore, the complex interplay between tree characteristics and disturbance regime and/or interactions may lead to peculiar assemblages of TreMs (Martin et al., 2021), and significantly contribute to the organization of post-disturbance arthropod communities (Chap. 6; Kozák et al., 2018, 2021). Likewise, species-specific physical and chemical characteristics of leaves differentially affect their flammability, e.g., long curly leaves containing high amounts of terpenes are highly flammable (Ormeño et al., 2009; Varner et al., 2015). Consequently, depending on dominant plant species, litter can be more or less severely affected by wildfires, which implies more or less extended impacts on soil arthropod communities (Verble-Pearson, 2014).

Pre-disturbance forest management

Pre-disturbance forest management can modulate disturbance regimes and stand susceptibility to disturbances (e.g., Jahani and Saffariha, 2021; Strith et al., 2021; Stueve et al., 2011; Suvanto et al., 2016 for windstorm, Castagneri et al., 2022; Elkin et al., 2015; Gobin, 2014; Manrique-Alba et al., 2022 for drought). For example, dense plantations of easily flammable species promote severe wildfires (Leverkus et al., 2022; Levine et al., 2022; Stephens and Moghaddas, 2005; Thompson et al., 2007). Conversely, landscape fuel reduction treatments can decrease wildfire severity and promote post-fire seedling regeneration (Tubbesing et al., 2019). Following a high intensity fire in south-eastern Australia, Bowd et al. (2021c) showed that old-growth forests recovered better than younger ones, because old-growth forests displayed a higher abundance of seed-tree species. Likewise, mixing tree species can affect stand susceptibility to windstorms (Torun and Altunel, 2020), and, depending on tree mixing characteristics, increase stand resistance to drought and wildfire (Jactel et al., 2017; Pardos et al., 2021). Mixing tree species also provides associational resistance to herbivores, i.e. to retroactions of arthropod communities to pulses of weakened hosts following disturbances (Jactel et al., 2017, 2021). The inflection of disturbance regimes by forest management could modulate the amount and diversity of disturbance legacies such as stand structure (e.g., complexity of vertical stratum), micro-environments and resources (e.g., soil, burned pieces of deadwood, etc.), with cascading effects on post-disturbance arthropod communities. Pre-disturbance management can also interact with disturbance regime and influence the amount of disturbance legacies. For instance green tree retention during harvest increased the amount of deadwood following prescribed fires, and promoted red-listed saproxylic insects (Hyvärinen et al., 2006).

Pre-disturbance forest management modulates the initial amount of microhabitats and trophic resources and consequently filters ecological traits in pre-disturbance arthropod communities, which may promote or hamper their resilience to disturbances. Thinning can reduce the amount of dead and living trees carrying large arrays of TreMs, or suitable for their differentiation (e.g., for snags, Cosyns et al., 2020; Courbaud et al., 2022; Larrieu et al., 2012; Paillet et al., 2019; Vuidot et al., 2011), but may also promote particular TreMs, such as bark injuries occurring during harvesting operations, or dendrotelms (Courbaud et al., 2022; Vuidot et al., 2011). As a result, thinning and logging may alter the initial supply of critical resources like deadwood and TreMs, and initial environmental conditions in the canopy and ground layers

through increased canopy openness. More generally, intensive forest management negatively affects the community of saproxylic arthropods (Grove, 2002; Stokland et al., 2012), and could therefore postpone their response to deadwood pulses following a disturbance. On the contrary, by regularly creating canopy gaps, forest management maintains populations of forest pollinators (Hanula et al., 2016), allowing them to rapidly exploit the post-disturbance pulses in floral resources (Heil and Burkle, 2018).

Pre-disturbance landscape matrix

Landscape matrix influences disturbance regimes. For instance, patterns of wildfire spread and severity are an interactive function of topography, vegetation, management and land use (Carlson et al., 2011; Carmo et al., 2011; Levine et al., 2022; Rogeau et al., 2018; Tubbesing et al., 2019; Turner, 2010; Turner et al., 1999). Likewise, large forest gaps increase the likelihood of windstorm damage at the landscape level (Harcombe et al., 2004; Panferov and Sogachev, 2008; Torun and Altunel, 2020). Forest edge exposure also results in a disruption of the microclimatic buffer and therefore exacerbates the effects of drought on vegetation and arthropod communities (De Frenne et al., 2021; Koelemeijer et al., 2022; Peguero et al., 2021; Šustek et al., 2017). Consequently, the landscape matrix can be seen as a mosaic of habitats more or less prone to disturbances. This will markedly influence the spatial distribution of disturbance refugia, and the recolonization processes by arthropod communities. High proportions of disturbance-prone forests at the landscape level could also lead to the development of "landscape traps" (Lindenmayer et al., 2022). These are situations where major functional and ecological attributes are compromised, and ecosystems are maintained in a compromised state or undergo a further regime shift in which an entirely new type of vegetation cover develops (i.e. regime shift, Johnstone et al., 2016; Lindenmayer et al., 2011, 2022).

2.4.2 Material and information legacies from past disturbances

Legacies from past natural disturbances

Past disturbances have been shown to directly influence current arthropod communities in forests through changes in forest structure. For instance, Kozák et al. (2021) showed that current saproxylic beetle assemblages are influenced by the historical disturbances that occurred over the last 250 years. Overall, the recency and the severity of the last disturbance increased the current species richness, although maximum disturbance severity had negative effects (Kozák et al., 2021). The changes in current insect assemblage were mainly mediated through changes in deadwood resources and canopy openness (Bače et al., 2017).

Legacies from past anthropogenic disturbances

Pre-disturbance conditions are also influenced by changes in land-use that occurred a long time ago. For example, Mollier et al. (2022) showed that forest area from 150 years ago is a better predictor of current beetle communities than present forest area. This is probably mediated by ancient forest legacies related to forest maturity and continuity (Janssen et al., 2017). Past land-use also significantly determined current forest vegetation, due to plant historically favored by human (Bebi et al., 2017; Conedera et al., 2017; Friedman and Reich, 2005), colonization credit (Hermy and Verheyen, 2007; Mollier et al., 2022), nutrient availability (e.g., generally higher in former agricultural lands, Fraterrigo et al., 2006), which largely affect the dynamics of the post-disturbance vegetation (Puerta-Piñero et al., 2012). Recent forests, less than 150 years old, are generally more frequently affected by disturbances than ancient forests, which affects the supply of legacies and consequently arthropod communities (Munteanu et al., 2015; Stritih et al., 2021).

2.5 Influence of post-disturbance forest management on disturbance legacies

2.5.1 Post-disturbance forest management: a range from active salvage logging to hands off management

Post-disturbance forest management encompasses a wide range of strategies ranging from intensive to passive management approaches (Duncker et al., 2012). Following disturbances, logging is a typical management strategy in production forests (Lindenmayer et al., 2008), which is also occasionally implemented in forests with a high conservation value (Chylarecki and Selva, 2016; Mikusiński et al., 2018; Orczewska et al., 2019). Salvage logging is the practice of extracting trees in disturbed forests to minimize the loss of economic timber (Lindenmayer and Noss, 2006). Sanitation felling aims at harvesting weakened trees to prevent the build-up of populations of opportunistic pests and a subsequent outbreak (Stadelmann et al., 2013). In contrast, the absence of active management, within the frame of a "benign neglect" or passive strategy, allows the retention of disturbance legacies (Müller et al., 2010). This last strategy is mostly implemented in conservation forests (Duncker et al., 2012; Horák et al., 2016; Müller et al., 2010; Thorn et al., 2017). In parallel, forest managers can implement different types of actions, through close-to-nature forestry or retention harvesting (Gossner et al., 2013; Hilszczański et al., 2016; Jaworski et al., 2019), to reach a compromise between total retention of legacies and total logging, by retaining a certain number of legacies (Duncker et al., 2012). These include the "benign neglect" strategy which allows naturally disturbed ecosystems to recover without human intervention.

2.5.2 Post-disturbance management and disturbance legacies

Common management strategy worldwide is salvage logging (Lindenmayer et al., 2008). It consists of the felling and extraction of affected trunks, often including the elimination of remaining branches, and it is arguably justified as a means to mitigate economic losses, reduce pest risks, or help restore the ecosystem (Müller et al., 2019). Whereas its effectiveness in mitigating subsequent disturbances remains unclear (Leverkus et al., 2021a), it constitutes a form of linked disturbance itself, as forests are more likely of being logged after a natural disturbance than in its absence (Leverkus et al., 2018a).

Surviving arthropods and colonisation patterns

Numerous studies have explored the effects of salvage and sanitation logging on arthropod communities (Thorn et al., 2018a). Salvage logging can affect species succession by disrupting colonization and recolonization patterns, and by affecting the community of surviving arthropods. For instance, the removal of deadwood legacies, propagules, and associated changes in micro-environmental conditions of deadwood resources and soil, negatively affect saproxylic arthropods, including those that survive within deadwood and those that subsequently colonize the substrate (Cobb et al., 2011; Georgiev et al., 2021, 2022; Hilszczański et al., 2016; Thorn et al., 2014, 2018a; Waldron et al., 2013), but also soil arthropods (Molinas-González et al., 2019). Conversely, logging promotes the colonization of disturbed areas by generalist species, and species associated with more open habitats and floral resources (Cours et al., 2021; Georgiev et al., 2021; Heil and Burkle, 2018; Phillips et al., 2006; Sire et al., 2022; Thorn et al., 2017, 2018a), and consequently induces shifts in the composition of arthropod communities (Wermelinger et al., 2017). Salvage logging can also disturb ecological relationships, such as species-resource relationships (Godeau et al., 2020) or functional networks between species (e.g., plant-pollinator interactions, Burkle et al., 2021), and can result in an extinction debt (i.e. a delay between the loss of a habitat and the local extinction of the species associated with that habitat; Cours et al., 2021). At a landscape scale, logging increases habitat diversity (undisturbed forests, disturbed and disturbed-harvest), and promotes the gamma-diversity of arthropod communities (Phillips et al., 2006; Wermelinger et al., 2017).

In contrast, the "benign neglect" strategy ensures the maintenance of disturbance legacies and of their associated arthropod species. Among these, compared to logged stands, saproxylic arthropods greatly benefit from the retention of deadwood following disturbances (Beudert et al., 2015; Cours et al., 2021, 2022; Georgiev et al., 2021; Grove, 2002; Müller et al., 2010; Thorn et al., 2015, 2018a). Furthermore, passive post-disturbance strategy also allows to maintain greater network connections between pollinators and plant species than salvage logging (Burkle et al., 2021). Even though logged areas are generally more favorable to open-habitat arthropod species compared to passively managed ones (e.g., Heil and Burkle, 2018 for bees), Galbraith et al. (2019) observed greater alpha and beta diversities of wild bees in unlogged areas than in logged ones.

Few studies considered the effects of intermediate forest management strategies after a natural disturbance, such as retention harvesting or close-to-nature forestry (Duncker et al., 2012; Leverkus et al., 2018a). Scattered trees or groves retained during clear-cuts generally support intermediate communities composed of both species from intact forest and clear-cut areas but do not support specialists (e.g., interior forest species, Fedrowitz et al., 2014; Lindenmayer et al., 2019). Even when retention levels are high, the community of saproxylic arthropods exhibit substantial changes compared to those of intact forests (Georgiev et al., 2022; Lee et al., 2018). According to Müller and Bütler (2010), minimum threshold values of 30 to 50 m³.ha⁻¹ are needed to ensure a relatively high richness of saproxylic organisms, and Thorn et al. (2020) found that 75% of disturbed forest areas need to be retained to maintain 90% of the species richness present in those disturbed areas.

Micro-environmental legacies: canopy openness and soil conditions

On a short time scale, post-disturbance logging operations further increase canopy openness (Foster and Orwig, 2006; Kendrick et al., 2015; Peterson and Leach, 2008), and induce shifts in arthropod communities towards species preferring warmer and sunnier environments (Bouget et al., 2013, 2014a; Georgiev et al., 2021; Phillips et al., 2006; Thorn et al., 2016c, 2018a).

The impact of logging on soil condition is highly context-dependent, and is influenced by logging intensity (Lucas-Borja et al., 2020; Martineau et al., 2020; Peterson and Leach, 2008). Increased canopy openness and the removal of downed deadwood generally increase soil temperatures, and decrease soil moisture (McIver and Starr, 2001). The removal of downed deadwood reduces the amount of available nutrients compared to stands where legacies are retained (García-Orenes et al., 2017; Juan-Ovejero et al., 2021; Marañón-Jiménez and Castro, 2013; Marañón-Jiménez et al., 2013; Pereg et al., 2018). The use of machinery generally increases soils compaction (García-Orenes et al., 2017; Lucas-Borja et al., 2020; Rab, 2004; Wagenbrenner et al., 2015) and, together with the removal of woody debris, it modulates the abundance and diversity of soil microsites and microtopography, with generally a decrease in pits and mounds but an increase in microsite richness (Peterson and Leach, 2008; Taerøe et al., 2019; Waldron et al., 2013, 2014). These effects can persist for a long time (e.g., 10 years in boreal forests, Kishchuk et al., 2015).

Resource pulses and collapses

Most disturbance legacies are affected by subsequent logging (Lindenmayer and Noss, 2006). Logging removes dead and weakened trees, and woody debris thereby affecting the succession patterns of saproxylic arthropods (Cobb et al., 2011; Cours et al., 2021; Lewis, 2009; Priewasser et al., 2013; Russell et al., 2006; Thorn et al., 2016c, 2018a; Waldron et al., 2013). The amount of deadwood in a stand generally remains high after post-disturbance logging (Cours et al., 2021; Georgiev et al., 2021, 2022; Merganič et al., 2022; Priewasser et al., 2013; Waldron et al., 2013), but the decrease is sufficient to affect arthropod biodiversity (Thorn et al., 2018a, 2020), and the diversity of deadwood resources is reduced (Waldron et al., 2013). For instance, rare types of disturbance-induced deadwood resources and microhabitats, like charred snags and logs, colonized by rare specialist species can be removed (Boucher et al., 2016; Hutto,

2006). This also affects the composition and diversity of TreMs (Chap. 4, Cours et al., 2021; Waldron et al., 2013). However, the magnitude of these negative consequences highly depends on disturbance severity and logging intensity themselves (Cours et al., 2021; Merganič et al., 2022).

While post-disturbance logging does not produce a generalized effect on the density or height of subsequent tree regeneration (Leverkus et al., 2021b), it can affect its composition (Taeroe et al., 2019). Logging often promotes early-successional resprouting species, but disfavors late-successional seeding species and their related arthropod species (Fidej et al., 2016; Jonášová and Prach, 2004; Leverkus et al., 2014; Michalová et al., 2017; Palik and Kastendick, 2009; Taeroe et al., 2019). However, these immediate effects generally fade in the longer term (Leverkus et al., 2021b; Royo et al., 2016; Sass et al., 2018, but see Morimoto et al., 2019).

Following post-disturbance harvest, different afforestation strategies can be implemented, from natural regeneration to full planting of new tree species. Shifting tree species may result in a major resource collapse for the community of phytophagous arthropods (Brändle and Brandl, 2001; Leiding et al., 2021; Vehviläinen et al., 2007), but also for those of saproxylophagous species (Müller et al., 2015; Seibold et al., 2022), at least for initial stages of the saproxylation process (Jonsell et al., 1998; Seibold et al., 2022). This would be particularly true if a native tree species is replaced by a non-native and phylogenetically and functionally distant tree species (Bouget et al., 2021; Mitchell et al., 2021, e.g., in boreal forests: Felton et al., 2020; Jonsell et al., 1998).

Changes in spatial patterns and heterogeneity

Logging can increase habitat fragmentation (Mikoláš et al., 2019; Mikusiński et al., 2018), especially those of disturbance refugia, thereby affecting the dispersal and colonization processes of arthropod species (Saint-Germain et al., 2013). Post-disturbance logging also leads to a considerable alteration of local deadwood composition and, as a result, increases β -diversity of saproxylic organisms across salvaged areas (Chap. 6, Georgiev et al., 2022). In addition, shifts in tree species during afforestation may increase habitat diversity at the landscape scale. This would also increase β - and γ -diversities of arthropod communities (Ampoorter et al., 2020; Brockerhoff et al., 2008).

2.5.3 Is there an optimal way to manage and limit the consequences of abiotic disturbances?

Post-disturbance forest management is at crossroads of ecological, economic and social contexts. In addition to ecological and economic risks management, salvage logging, sanitation felling, and retention forestry could also pursue a recreational objective by securing hiking areas. Kortmann (2022) showed that forests heavily disturbed by bark beetle outbreaks in the Bavarian Forest National Park were still very popular with visitors. However, post-disturbance logging considerably alters disturbance legacies, their associated arthropod communities, and the successional process. The optimal way to manage disturbed areas is therefore highly context dependent (Hlásny et al., 2021a). In both intensively managed and multifunctional forests, it appears unnecessary to harvest weakened and dead trees while harvesting costs are higher than the selling price (Eklund et al., 2009; Kortmann, 2022). For instance, only easily accessed trees, close to roads and tracks, could be harvested to reduce economic losses and secure roads and paths (Eklund et al., 2009). Overall, sanitation felling could be limited to a restricted proportion of disturbed forest areas at the landscape-scale, to prevent bark beetle outbreaks (Augustynczyk et al., 2021). Maximizing the retention of disturbance legacies limits the detrimental effects of logging on biodiversity and subsequent successional process. Therefore, passive management or full legacy retention should become an increasingly common response to disturbances, especially when timber prices are decreasing significantly due to market pulses (Hlásny et al., 2021b).

2.6 Synthesis, conclusions and future research directions

Shifts in disturbance regime may lead to misalignments between the effects of a disturbance and the ecological memory of an ecosystem (Johnstone et al., 2016). This affects the disturbance legacies, thereby compromising the resilience of the ecosystem (Johnstone et al., 2010, 2016, 2020). For instance, a recent shift in disturbance regime in Alaska towards more severe wildfires led to a modification of the plant community from coniferous to deciduous species (Johnstone et al., 2010, 2016).

Several shifts in disturbance regimes occurred in forest ecosystems during the last centuries, with sometimes major ecological impacts (Brook et al., 2013; Ellis, 2011; Sprugel, 1991; Turner, 2010). However, the speed of current changes in disturbance regimes appears to be unprecedented and largely questions the future of world's forests and their associated communities (Parmesan et al., 2022). The frequency, intensity and spatial extent of droughts, wildfires and windstorms, as well as their interactions, have been increasing exponentially in temperate forests worldwide during the last decades, due to climate and land-use changes and intensification (Allen et al., 2010; Dale et al., 2001; Gregow et al., 2017; Halofsky et al., 2020; Hammond et al., 2022; McDowell et al., 2020; Seidl et al., 2017; Senf and Seidl, 2021c; Senf et al., 2020; Turner, 2010). And major ecological consequences are expected in forest ecosystems, including global forest rejuvenation, loss of old-growth forests, and even shifts from forest to non-forest ecosystems (Johnstone et al., 2016; McDowell et al., 2020; Turner, 2010; Turner et al., 2021).

Part II

Consequences of forest diebacks on habitat structures

Dieback effects on dead wood: large scale trends from cross-analysis of European forest databases

C. BOUGET , C. BARD, J. COURS 

The full chapter is in appendix [A](#).

Abstract

Deadwood is a particularly rare habitat in European managed forests, although it supports a high level of biodiversity. However, forest dieback, due to natural disturbances exacerbated by current climate change, could increase the stock of deadwood in managed forests. This increase is expected to depend on several factors associated with the disturbance, e.g. its intensity, or the forest stand, e.g. tree species or forest management.

We used a time series of annual defoliation surveys of European forests to characterise the dieback phenomenon. In addition, we used data from a study carried out between 2006 and 2009 on the amount of dead wood present on the same survey plots. The total amount of dead wood was broken down by diameter and decay. We focused on the ten years of defoliation survey before measuring dead wood in order to maintain a large number of survey plots.

We showed that the average level of defoliation in the five years prior to the deadwood survey increased the amount of deadwood. At the same time, the longer the time since the last defoliation peak, the less dead wood there was. However, these effects were concentrated on fresh deadwood, decayed deadwood was not affected by decay in the ten years prior to the measurement and therefore seems to require longer time series.

We shown that the stock of deadwood in European forests is significantly affected by dieback.

Keywords: Forest dieback; Dead wood; Disturbance legacy; Climate change; Global scale

Résumé

Le bois mort est un habitat particulièrement rare dans les forêts européennes gérées alors qu'il abrite une grande biodiversité. Néanmoins, le dépérissement des forêts, dû à des perturbations naturelles exacerbées par le changement climatique actuel, pourrait augmenter le stock de bois mort dans ces forêts gérées. Cette augmentation devrait dépendre de plusieurs facteurs associés aux perturbations, e.g. leur intensité, ou au peuplement forestier, e.g. les espèces d'arbres ou la gestion forestière.






Nous avons utilisé une série chronologique d'enquêtes annuelles sur la défoliation des forêts européennes pour caractériser le phénomène de dépérissement. En outre, nous avons utilisé les données d'une étude réalisée entre 2006 et 2009, sur les quantités de bois mort présentes sur les mêmes placettes d'enquête. La quantité totale de bois mort a été déclinée en fonction du diamètre et de la décomposition. Nous nous sommes concentrés sur les dix années d'étude de la défoliation avant mesure du bois mort afin de maintenir un grand nombre de placettes.

Nous avons ainsi montré que le niveau moyen de défoliation dans les cinq années précédant le relevé du bois mort augmentait la quantité de bois mort. Parallèlement, plus le temps s'écoule depuis le dernier pic de défoliation, moins il y a de bois mort. Cependant, ces effets se sont concentrés sur le bois mort frais, le bois mort décomposé n'a pas été affecté par le dépérissement dans les dix années précédant la mesure et semble donc nécessiter de plus longues séries chronologiques.

Nous avons montré que le stock de bois mort dans les forêts européennes est significativement affecté par le dépérissement.

Mots-clés : Dépérissement forestier; Bois mort; Héritage de perturbation; Changement climatique; Echelle globale

Trait-based response of dead wood and tree-related micro-habitats to dieback in temperate forests

C. BOUGET , J. COURS , V. SPECKENS, L. LARRIEU , A. SALLÉ , G. PARMAIN 

The full chapter is in appendix [B](#).

Abstract

Deadwood and tree-related microhabitats (TreMs) are affected by forest management and are therefore relatively rare in managed European forests. Senescence and tree mortality resulting from forest dieback should provide these habitats. However, these contributions are expected to be highly context-dependent (e.g. due to tree species or type of disturbance affecting tree vitality).

We used study plots established along a gradient of forest dieback in two distinct contexts: fir-dominated forests (*Abies alba*) in the French Pyrenean mountains, and oak-dominated forests (*Quercus* spp.) in the Loire valley, in the lowlands. Dieback in both contexts was mainly triggered by successive drought events. In these study plots we recorded living and dead trees using a relascope protocol. We recorded the species, diameter and decomposition in case of dead wood. Finally, we listed the TreMs present on each tree.

We shown that forest dieback influences both dead wood and TreMs profiles. The amount of dead wood generally and significantly increased due to dieback. Similarly, tree injury and saproxylic fungi were positively affected by dieback. We showed that changes in TreMs profiles were due to changes in deadwood profiles.

Forest dieback increased the amount of dead wood and changed the profiles of the TreMs so that the habitats generated are closer to those associated with old growth forests.

Keywords: Forest dieback; Dead wood; Tree-related microhabitats; Disturbance legacy; Forest management

Résumé

Le bois mort et les dendromicrohabitats (TreMs) sont affectés par la gestion forestière et sont donc relativement rares dans les forêts européennes gérées. La sénescence et la mortalité des arbres résultant du dépérissement de la forêt devraient fournir ces habitats. Néanmoins, ces contributions devraient être fortement dépendantes du contexte (par exemple, en raison de l'espèce d'arbre ou du type de perturbation affectant la vitalité de l'arbre).

Nous avons utilisé des placettes d'étude établies le long d'un gradient de dépérissement forestier dans deux contextes distincts : des forêts à dominante de sapins (*Abies alba*) dans les montagnes pyrénéennes françaises, et des forêts à dominante de chênes (*Quercus* spp.) dans la vallée de la Loire, en plaine. Le dépérissement dans les deux contextes a été principalement déclenché par des événements de sécheresse successifs. Dans ces placettes d'étude, nous avons enregistré les arbres vivants et morts en utilisant un protocole relascopique. Nous avons noté l'espèce, le diamètre et l'état de décomposition en cas de bois mort. Enfin, nous avons listé les TreMs présents sur chacun d'entre-eux.

Nous avons montré que le dépérissement forestier influence à la fois les profils de bois mort et de TreMs. La quantité de bois mort a généralement et significativement augmenté en raison du dépérissement. De même, les blessures des arbres et les champignons saproxyliques ont été positivement affectés par le dépérissement. Nous avons montré que les changements dans les profils de TreMs étaient dus aux changements des profils de bois mort.

Le dépérissement forestier a augmenté la quantité de bois mort et a modifié les profils des TreMs de sorte que les habitats engendrés se rapprochent de ceux liés aux vieilles forêts.

Mots-clés : Dépérissement forestier; Bois mort; Dendromicrohabitats; Héritages de perturbation; Gestion forestière

Part III

Consequences of local forest dieback on biodiversity and mediation by habitat change and human interventions

Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests

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Highlights

- We examined effects of dieback and salvage logging in two montane coniferous forests.
- The composition of saproxylic beetles seemed highly modified by severe diebacks.
- The severity and spatial extent of diebacks seemed to influence the beetles response.
- The more severe the dieback, the greater the deadwood amount and the canopy opens.
- We invite foresters to conserve biological legacies through deadwood-rich areas.

Abstract

Natural disturbances are major drivers of forest dynamics. However, in the current context of anthropogenic global warming, shifts in disturbance regimes are expected. Natural disturbances usually leave biological or structural legacies which are important for early-successional species. Nevertheless, these legacies are usually eliminated by forest managers through salvage logging. Here, we investigated the consequences of forest dieback and the following salvage logging on both forest habitat conditions and saproxylic beetle communities.

We conducted our study in two types of conifer-dominated highland forests: Pyrenean silver fir (*Abies alba*) which has suffered drought-induced dieback and Bavarian Norway spruce (*Picea abies*) which has suffered bark beetle-induced (*Ips typographus*) dieback.

In both of the forest contexts, dieback provided a biological legacy through an increase in deadwood resources; however, this increase was much greater in the spruce forests. Nonetheless, despite this increase in resources, neither type of forest gained in total abundance or species richness after disturbance, compared to healthy stands. Nevertheless, the species composition of saproxylic beetle composition was significantly affected by dieback in spruce stands, but not in the silver fir forests. In the spruce plots, saproxylic beetles responded positively to the large increase in deadwood in the declining stands, including a very strong positive response from red-listed species. Saproxylic beetle assemblages in spruce forests were mainly driven by canopy openness and deadwood amount. In the silver fir plots, we did not observe responses from the saproxylic beetle communities to deadwood amount increase. This lack of response may be explained by the relatively low amount of deadwood generated by the drought-induced dieback.

Concerning salvage logging, it caused stronger contrasts in spruce forests than in silver fir forests, where it generally had no significant impact. For example, in spruce forests, salvage logging reduced the density of large snags by 91% and large logs by 87% compared with unharvested declining plots. Most of the significant environmental effects on biodiversity associated with dieback were no longer significant after accounting for the salvaged plots in our study data.

Then, forest dieback and salvage logging induced much sharper and stronger effects on environmental and community metrics in the spruce than in the silver fir forests. The contrast between Bavaria and the French Pyrenees seems partly related to dieback severity. Finally, we invite forest managers to conserve biological and structural legacies through patches of deadwood-rich areas.

Keywords: Forest dieback; Salvage logging; Saproxylic beetles; Deadwood; Climate change; Drought; Bark beetles; Biological legacy; Early-successional forest

Résumé

Les perturbations naturelles sont des composantes majeures des dynamiques forestières. Cependant, dans le contexte actuel de réchauffement global anthropique, des changements importants des régimes de perturbation sont attendus. Les perturbations naturelles laissent généralement des héritages biologiques et structurelles qui sont cruciaux pour les espèces de début de succession. Néanmoins, ces héritages sont traditionnellement éliminés par les gestionnaires forestiers aux travers de coupes de récupération. Dans cette étude, nous avons étudié les conséquences des dépérissements forestiers et des coupes de récupération qui s'ensuivent sur les conditions d'habitat et les communautés de coléoptères saproxyliques.

Nous avons conduit notre étude dans deux types de forêts de montagne à dominance résineuse: les sapinières pyrénéennes (*Abies alba*) qui ont souffert de sécheresses, et les pessières bavaroises (*Picea abies*) qui ont souffert d'épidémies du scolyte typographe (*Ips typographus*).

Dans les deux contextes forestiers, le dépérissement a fourni des héritages biologiques sous la forme d'une augmentation des ressources en bois mort; cependant, cette augmentation était bien plus importante dans les forêts d'épicéas. Néanmoins, malgré cette augmentation de ressource, aucun des contextes forestiers n'avait gagné d'abondance totale ou de richesse spécifique après dépérissement, en comparaison des peuplements sains. En revanche, les compositions en espèces de coléoptères saproxyliques étaient significativement affectées par le dépérissement dans les peuplements d'épicéas, mais pas dans les peuplements de sapins pyrénéens. En pessière, les coléoptères saproxyliques ont répondu positivement à l'importante augmentation du bois mort dans les peuplements dépérissants, incluant une très forte réponse positive des espèces classées sur liste rouge. Les assemblages de coléoptères saproxyliques dans les peuplements d'épicéas étaient principalement déterminés par l'ouverture de la canopée et la quantité de bois mort. Dans les peuplements de sapins; nous n'avons pas observé de réponses de la part des communautés de coléoptères saproxyliques, à l'augmentation de bois mort. Ce manque de réponse peut s'expliquer par la quantité relativement faible de bois mort généré par le dépérissement induit par la sécheresse.

Les coupes de récupération ont provoqué des contrastes plus forts dans les forêts d'épicéas que dans les forêts de sapins, où il n'a généralement pas eu d'impact significatif. Par exemple, dans les forêts d'épicéas, les coupes de récupération ont réduit les densités des chandelles de gros diamètre de 91% et des grosses pièces de bois mort au sol de 87%, en comparaison des peuplements dépérissants non-exploités. La plupart des effets environnementaux significatifs sur la biodiversité associée au dépérissement n'étaient plus significatifs après avoir pris en compte les coupes de récupération.

Par conséquent, le dépérissement forestier et les coupes de récupération ont induit des effets beaucoup plus marqués et forts sur les paramètres environnementaux et de communautés dans les peuplements d'épicéas que dans les peuplements de sapins. Le contraste entre la Bavière et les Pyrénées françaises semble en partie lié à la sévérité du dépérissement. Enfin, nous invitons les gestionnaires forestiers à conserver les héritages biologiques et structurels par le biais d'îlots riches en bois mort.

Mots clés: Dépérissement forestier; Coupe de récupération; Coléoptères saproxyliques; Bois mort; Changement climatique; Sécheresse; Scolytes; Héritage biologique; Forêt en début de succession

5.1 Introduction

Natural disturbances such as droughts, storms or pest outbreaks are major drivers of forest dynamics (Chapin et al., 2011; Pickett and White, 1985). However, in the current context of anthropogenic global warming, shifts in disturbance regimes are expected (Sallé et al., 2014; Samaniego et al., 2018). Droughts in Europe will increase in area, duration and frequency as a result of global warming (Samaniego et al., 2018). Higher temperatures are likely to have direct positive impacts on insect pest species through lower winter mortality and higher voltinism (Bale et al., 2002; Jönsson et al., 2009), and distribution ranges are shifting northward (Robinet et al., 2007). Since climate change is more rapid in mountain regions (twice as fast as in other terrestrial regions; Auer et al., 2007), upland forests are important sentinels for monitoring.

Though the consequences of disturbances are often deemed destructive in terms of habitat, leading to "biodiversity loss" (Lehnert et al., 2013), from a conservation perspective, natural disturbances could have a positive impact on forest habitats and associated biodiversity (Kulakowski et al., 2017; Lindenmayer et al., 2006; Swanson et al., 2011; Thorn et al., 2017). Natural disturbances leave biological and/or structural legacies (i.e. *"the organisms, organic materials, and organically-generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem"*; Franklin et al., 2000), which depend both on the forest characteristics prior to the disturbance and on the disturbance itself. For example, the main biological legacies from bark beetle outbreaks and windstorms are respectively snags (standing dead trees) and logs (downed dead trees), both of which lead to an overall increase in deadwood amount and in stand structural heterogeneity on a large spatial scale (Swanson et al., 2011; Thorn et al., 2017).

Forest managers usually respond to such natural disturbances with salvage logging in order to recover the economic value that would otherwise be lost but also to control insect pests by removing infected trees (Lindenmayer et al., 2008; Müller et al., 2019; Thorn et al., 2018a). Thus, natural disturbances could supply more resources (i.e. deadwood) for some organisms such as saproxylic insects, which are particularly at risk in heavily managed forests (Grove, 2002; Stokland et al., 2012), while salvage logging would affect them negatively (Thorn et al., 2018a). Indeed, by avoiding the recruitment of biological legacies such as large dying trees, snags and logs, salvage logging reduces saproxylic habitat and connectivity, and homogenizes landscape configuration (Leverkus et al., 2020; Lindenmayer et al., 2008; Thorn et al., 2018a).

Since biological and structural legacies appear to be very important for the recruitment of early-successional species (e.g. Fontaine et al., 2009; Kortmann et al., 2018a for birds; Wentzel et al., 2019 for

bats; [Thorn et al., 2016c](#) for arthropods and [Thom and Seidl, 2016](#) for a broader perspective), it seems very important to retain specific legacies after natural disturbances. However, the current lack of studies on how different sources of disturbance change habitat conditions and, as a result, biodiversity, does not allow us to identify important biological and structural legacies.

We investigated the effects of two types of forest dieback followed by salvage logging on both habitat conditions and saproxylic beetle communities, a group that we expected to respond to natural disturbances modifying the habitat (canopy opening, amount of deadwood; [Bouget et al., 2014a](#); [Lassauce et al., 2011](#)). We studied forest dieback caused by (i) warming-related drought stress in forests dominated by silver fir (*Abies alba* Mill.) in the French Pyrenees ([Camarero et al., 2011](#)), and by (ii) bark beetle outbreaks (following a windstorm in Bavarian Norway spruce forests (*Picea abies* (L.) H.Karst.); [Müller et al., 2008, 2010](#); [Thorn et al., 2014](#)).

Firstly, we analysed the effects of the two types of natural disturbances plus the anthropogenic disturbance (i.e. salvage logging) on habitat conditions. Secondly, we studied the effect of the disturbance and salvage logging on the saproxylic beetle communities in the forest.

Finally, we proceeded to a broader ecological analysis by addressing three questions:

1. Do effects on saproxylic beetle community metrics relate to a change in habitat quantity or heterogeneity caused by disturbances?
2. Are the ecological relations between environmental conditions and saproxylic beetle community observed under forest dieback process still significant after salvage logging operations?
3. Do saproxylic beetle communities react in the same way to the changing environments in both studied contexts of natural disturbance (drought stress and bark beetle outbreaks) ?

5.2 Materials and methods

5.2.1 Study area and study sites

The study was conducted in two types of conifer-dominated highland forests undergoing severe dieback: silver fir forests in the Pyrenees (southwestern France) and Norway spruce forests in Bavaria (southeastern Germany; Fig. 5.1).

In France, the study plots were divided into two distinct zones (Fig. 5.1): 17 plots in the Aure Valley in Central Pyrenees (960–1481 m a.s.l., 1265 m on average), and 19 on the Sault Plateau in the Eastern Pyrenees (705–1557 m a.s.l., 1013 m on average). Forests cover 50% of the Aure Valley area and 73% of the Sault Plateau area. Silver fir stands occupy 50% and 75% of the two forest areas, respectively. In the study plots, dieback mainly occurred after the 2003 drought.

In Germany, 29 study plots were installed in the Bavarian Forest National Park (660 m to 1352 m above sea level, 1084 m on average). Forests cover about 98% of the Park area ([Bässler et al., 2009](#)). In hilly and higher montane sites, more than 80% of the forests are dominated by Norway spruce (*Picea abies* (L.) H. Karst), whereas in lower altitudes, forests are a mix of Norway spruce (58%) and three main secondary species: common beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and mountain ash (*Sorbus aucuparia* L.). In the Bavarian plots, forest dieback was mainly caused by massive outbreaks of the bark beetle *Ips typographus* L. (Coleoptera, Curculionidae, Scolytinae), which occurred in 2001 (± 5 years) in unharvested plots and in 2009 (± 4 years) in salvaged plots.

In both countries, the plots were divided into three categories: undisturbed forests ("healthy"), unharvested disturbed forests ("disturbed") and harvested (salvage logging) disturbed forests ("salvaged"; Fig. 5.1).

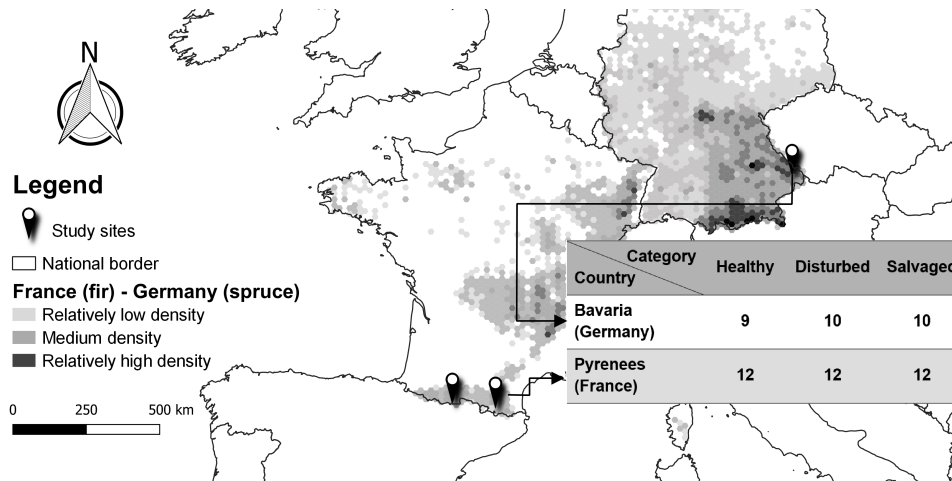


Figure 5.1 – Map showing the study sites in Germany (Bavaria) and in France (Pyrenees) and the number of plots for each country and each stand category. Mapping was performed in QGIS 3.10. Hexagonal binning was based on GBIF data for *Abies alba* in France and for *Picea abies* in Germany (GBIF.org, 2020).

5.2.2 Beetle sampling and identification

We sampled saproxylic beetles with one (Bavaria) or two (Pyrenees) flight–interception traps per plot. The traps consisted of a crossed pair of transparent plastic shields (40 × 60 cm) above a funnel leading into a container with an unbaited preservative (50% propylene glycol and 50% salt water with detergent). The traps were hung roughly 1.5 m above the ground in the centre of each plot from April to October for one sampling year only, in 2016 in Bavaria and in 2017 in the French Pyrenees. All the saproxylic beetles collected were identified to the highest possible taxonomic level (French dataset: G.P. and external experts; German dataset: Alexander Szallies). For the sake of balance, we drew a random subset of one trap per plot in the Pyrenean dataset *a posteriori*.

5.2.3 Species traits

We used the FRISBEE database to characterise species ecological traits: feeding guilds (zoophagous, xylophagous, saproxylophagous) and substrate guilds (cavicolous, xylofungicolous, flower-visitor) (Bouget et al., 2019). To distinguish between rare and common species, we used the FRISBEE database for French data (rare species have a patrimonial value ≥ 3 ; Brustel, 2001) and the red list status for Bavarian data (species are classified as "rare" if above the "of least concern" IUCN category; Seibold et al., 2015; Tab. 5.1).

We extracted quantitative niche trait values from Gossner et al. (2013) and Janssen et al. (2017) for preferences in terms of deadwood diameter, deadwood decay stage and forest canopy openness. For each plot and each niche trait, we calculated two multidimensional indices: community-level weighted means (CWM), defined as the mean of the trait values weighted by the relative abundance of each species bearing each value; and functional dispersion (FD), i.e. the mean distance of each individual species from the weighted centroid of all species in the assemblage (dbFD function, FD R-package; Laliberté et al., 2014).

5.2.4 Environmental variables

Stand variables associated to living and microhabitat-bearing trees were measured according to standardized protocols, whereas deadwood metrics were assessed with slightly different methods in the two regions.

Table 5.1 – Overview of the response variables used in our study (mean and range in Bavarian Norway spruce and Pyrenean silver fir datasets); CWM = Community-Weighted Means; FD = Functional Dispersion; rare species = patrimonial value ≥ 3 in France and red-listed in Germany.

Variable name	Short description	Pyrenees (silver fir)		Bavaria (Norway spruce)	
		Mean \pm se	Range (min - max)	Mean \pm se	Range (min - max)
Total Ab.	Abundance of all saproxylic beetles	451 \pm 46	74–1517	120 \pm 15	19–304
Total SR	Species richness of all saproxylic beetles	58 \pm 2	37–93	32 \pm 2	10–57
Rare sp. Ab.	Abundance of rare saproxylic beetles	11.4 \pm 3.1	0–104	8.2 \pm 2	0–37
Rare sp. SR	Species richness of rare saproxylic beetles	3.8 \pm 0.3	0–9	2.7 \pm 0.5	0–9
CWM wood diameter	Mean trait value of deadwood diameter preference	2.24 \pm 0.03	1.9–2.5	2.31 \pm 0.05	1.26–2.58
FD wood diameter	Trait variance of deadwood diameter preference	0.53 \pm 0.03	0.18–0.98	0.67 \pm 0.03	0.3–1.13
CWM wood decay	Mean trait value of deadwood decay preference	2.53 \pm 0.05	2.04–3.25	2.94 \pm 0.06	2.04–3.25
FD wood decay	Trait variance of deadwood decay preference	0.71 \pm 0.03	0.37–0.96	0.79 \pm 0.04	0.32–1.19
CWM canopy	Mean trait value of canopy-openness preference	1.68 \pm 0.02	1.37–1.88	1.84 \pm 0.03	1.58–2.22
FD canopy	Trait variance of canopy-openness preference	0.74 \pm 0.03	0.36–1.17	0.92 \pm 0.05	0.32–1.47
Cavicol. Ab.	Abundance of strict cavicolous beetles	24.5 \pm 2.9	3–76	8.7 \pm 1.4	1–33
Cavicol. SR	Species richness of strict cavicolous beetle	7.2 \pm 0.5	2–13	3.4 \pm 0.4	1–9
Xylofungicol. Ab.	Abundance of strict xylofungicolous beetles (all the species living in fungi, whatever the trophic guild)	96 \pm 9	25–245	34 \pm 9	4–264
Xylofungicol. SR	Species richness of xylofungicolous beetle	21 \pm 1	7–33	12.5 \pm 1	4–27
Floricol. Ab.	Abundance of flower-visiting beetles	12.6 \pm 1.7	3–57	35 \pm 6.5	1–129
Floricol. SR	Species richness of flower-visiting beetles	6 \pm 0.5	1–15	7 \pm 0.7	1–15
Zoophag. Ab.	Abundance of zoophagous beetles	84 \pm 10	19–227	42 \pm 6.5	4–135
Zoophag. SR	Species richness of zoophagous beetles	21.6 \pm 1.1	13–41	11.5 \pm 1	3–24
Conif. Xyloph. Ab.	Abundance of conifer xylophagous beetles	105 \pm 25	6–836	25 \pm 6.8	1–175
Conif. Xyloph. SR	Species richness of conifer xylophagous beetles	6.4 \pm 0.4	2–12	5 \pm 0.6	1–16
Pest sp. Ab.	Abundance of pest species	42 \pm 10	1–310	23 \pm 7	1–174

Firstly, we applied a relascope sampling protocol in Bavaria and the Pyrenees to record living or dying trees (≥ 17.5 cm in DBH), dead trees, snags (> 4 m in height; DBH ≥ 7.5 cm), and high stumps (height < 4 m and > 1 m; DBH ≥ 7.5 cm). Relascope sampling is characterized by a variable sampling radius and the use of a dendrometer linked to a basal area factor (one in the case of our study; [Bitterlich, 1984](#); [Piqué et al., 2011](#)). In relascope sampling, the probability that each tree is included in the plot is proportional to its diameter ([Piqué et al., 2011](#)). For each element, we recorded DBH, tree species, status (living tree, dying tree, snag, high stump, log), decay class for deadwood (4 categories from fresh deadwood to significantly decayed deadwood), and TreMs (tree-related microhabitats) borne on living trees and snags. All variables whose name ends with "0.3 ha" were evaluated with the relascope sampling protocol, 0.3 ha being the approximate area explored with the method (Tab. 5.2).

In addition, in both regions, we applied a protocol related to the Index of Biodiversity Potential ([Gosselin and Larrieu, 2020](#); [Larrieu and Gonin, 2008](#)) to perform an exhaustive survey of tree-related microhabitats (TreMs; [Larrieu et al., 2018](#)), large deadwood pieces (snags and logs ≥ 37.5 cm in diameter 1 m from the largest end) and number of strata covering $\geq 20\%$ of the area in a 1-ha circle centred on

each plot. Canopy openness, defined as the total proportion of open area providing flower resources, was also assessed in this 1-ha plot. Variables whose name ends with "1ha" were assessed with this protocol (Tab. 5.2).

Table 5.2 – Overview of the environmental predictors used in our study (mean and range in Bavarian Norway spruce and Pyrenean silver fir datasets); DW = deadwood; TreM = Tree-related Microhabitat.

Predictor name	Short description	Unit	Pyrenees (silver fir)		Bavaria (Norway spruce)	
			Mean \pm se	Range (min - max)	Mean \pm se	Range (min - max)
DW vol. 0.3 ha	Total volume of deadwood in a 0.3-ha plot	m ³ .ha ⁻¹	51 \pm 9	3–220	125 \pm 25	0.5–435
Snag vol. 0.3 ha	Volume of standing deadwood (> 7.5 cm in diameter) in a 0.3-ha plot	m ³ .ha ⁻¹	19 \pm 4	0–106	60.5 \pm 15	0–325
Snag density 1 ha	Number of large standing deadwood pieces (> 37.5 cm in diameter) in a 1-ha plot	nb.ha ⁻¹	8.6 \pm 1.3	0–34	34 \pm 7.5	1–129
Log vol. 0.3 ha	Volume of downed deadwood (> 17.5 cm in diameter) in a 0.3-ha plot	m ³ .ha ⁻¹	32 \pm 6	0–151	65 \pm 13	0–220
Log density 1 ha	Number of large lying deadwood pieces (> 37.5 cm in diameter) in a 1-ha plot	nb.ha ⁻¹	13.9 \pm 1.4	3–36	25 \pm 5	1–88
DW diversity 0.3 ha	Number of deadwood types (tree species*diameter*decay*position)	nb	7.6 \pm 0.8	1–27	7.5 \pm 0.7	1–15
Dead trees rel. BA 0.3 ha	Proportion of dead trees in total basal area in a 0.3-ha plot	%	6.2 \pm 1.1	1.3–32.3	32 \pm 7	1.7–98.3
Dead trees BA 0.3 ha	Basal area of dead trees (snags) in a 0.3-ha plot (> 10 cm in diameter)	m ² .ha ⁻¹	3.6 \pm 0.6	0–14	10.8 \pm 2.4	0–46
Living trees BA 0.3 ha	Basal area of living trees in a 0.3-ha plot (\geq 17.5 cm in diameter)	m ² .ha ⁻¹	30.4 \pm 2	15–66	16.7 \pm 3.6	0–61
Canopy openness 1 ha	Cumulative proportion of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants) in a circular 1-ha plot	%	26 \pm 4	1.8–79	52 \pm 7	2.5–98
Sapro TreM density 1 ha	Total density of saproxylic microhabitat-bearing trees in a 1-ha plot	nb.ha ⁻¹	3.7 \pm 0.7	0–22	1.9 \pm 0.45	0–8
Sapro TreM diversity 1 ha	Diversity of saproxylic microhabitat in a 1-ha plot	nb	3.3 \pm 0.3	0–7	1.8 \pm 0.3	0–5
Polypore density 0.3 ha	Density of fungus-bearing trees in a 1-ha plot (fruiting bodies of tough or pulpy saproxylic fungi)	nb.ha ⁻¹	26 \pm 8	0–249	39 \pm 9	0–283
Cavity density 1 ha	Density of cavity-bearing trees in a 1-ha plot (woodpecker breeding and feeding holes, cavities with mould with an entrance above 10 cm in width)	nb.ha ⁻¹	2 \pm 0.5	0–14	1.3 \pm 0.35	0–6

Among a list of 47 TreM types recorded (Larrieu et al., 2018), we selected a subset known to be important to saproxylic beetles (Stokland et al., 2012) and left out epiphytic structures (like mistletoe) and buttress-root concavities (Larrieu et al., 2018).

Downed log volume was based on the census from the relascope sampling method in the Pyrenees, and on data from the fixed-area plots (0.1 ha) in Bavaria. Fixed-area protocol is characterized by a fixed sampling radius and an equal probability that each tree is included in the plot (Piqué et al., 2011). We defined deadwood diversity as the number of combinations crossing the following deadwood features: status (lying or standing deadwood, crown deadwood), decay stage, diameter class and tree species, as suggested by Siitonen et al. (2000).

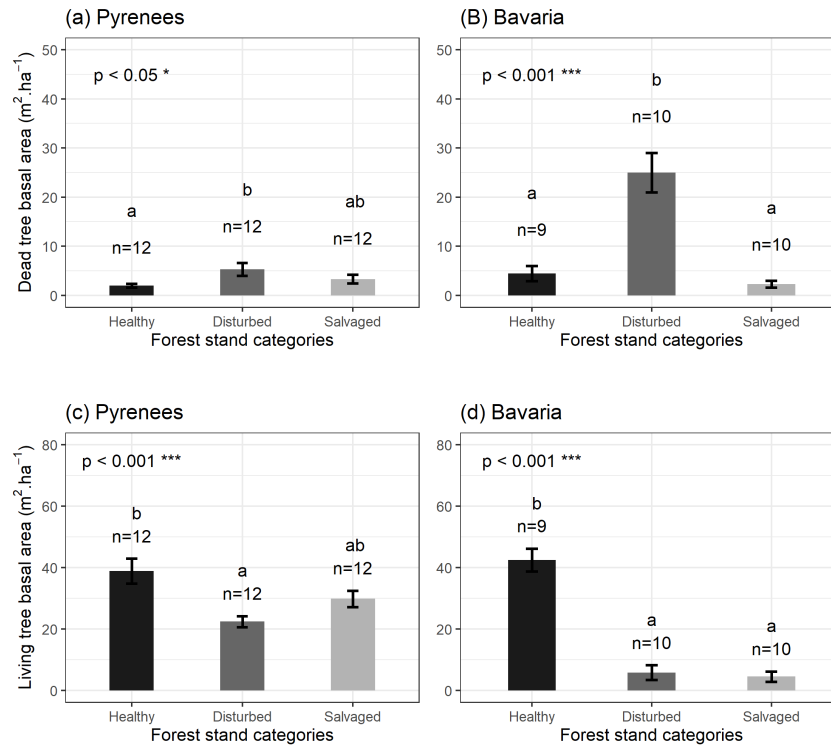


Figure 5.2 – Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) of dead trees (a, b) and living trees (c, d) in the 0.3-ha plots for each country and each stand category. Dead trees (snags) more than 7.5 cm in diameter are included. Letters indicate significant differences between each category (p value top-left). The letters result from post-hoc Tukey tests on generalized (negative binomial) linear mixed models.

5.2.5 Statistical analysis

Data analysis was conducted with R software 4.0.0 (R Core Team, 2022). In each country, we split our dataset into two subsets to study two different processes and their effects on forest stand features and on saproxylic beetle communities (Fig. S5.1): the "dieback" subset merging healthy and declining plots to assess the dieback effect, and the "salvage" subset merging declining and salvaged plots to test the effect of salvage logging operations.

For each response variable (abundance and species richness of feeding and substrate guilds, niche trait guilds, abundance and species richness of saproxylic beetles as a whole and of rare or red-listed species), we first selected the best fitting error structure with the `fitdist` function from the `fitdistrplus` R-package (Delignette-Muller et al., 2019). For the French data, we implemented generalized linear mixed models with "site" (Aure Valley or Sault Plateau) as a random variable (`glmmTMB` R package; Magnusson et al., 2020) to deal with "over-dispersion" for count variables (Bates et al., 2020). For the Bavarian dataset, as we only analysed a single geographical location, we used "glm" and "glm.nb" (MASS R package) in case of "over-dispersion" (Ripley et al., 2020).

We explored the influence of forest stand features associated to dieback or salvage logging effects (Fig. S5.1) on a subset of non-collinear variables (log of "Snag vol. 0.3 ha", "Lying dead wood diversity", "Log density 1 ha", "Canopy openness 1 ha", "Sapro TreM density 1 ha", "Sapro TreM density 0.3 ha", "Living trees BA 0.3 ha"; "check_collinearity" function, performance R-package; Lüdecke et al., 2020). We then selected the best model for each saproxylic beetle guild in the "dieback" subset ("dredge" function, MuMin R-package; Bartoń, 2020). In a second step, we ran each best model on data from the "salvage"

subset only to check if the environmental effects related to dieback were still significant after salvage logging (Fig. S5.1). We extracted parameter estimates and p-values ("model.avg" function, MuMin R package) and carried out a Holm p.value adjustment ("p.adjust" function).

To determine if the species composition of saproxylic beetle assemblages was influenced by dieback category (i.e. "healthy", "unsalvaged declining" and "salvaged declining" plots) and stand features, we performed NMDS (Nonmetric Multidimensional Scaling) and CAP (Canonical Analysis of Principal coordinates) ordinations and PERMANOVA analyses (Anderson and Walsh, 2013), based on between-plot Bray-Curtis distance matrices (vegan R-package; vegdist, metaMDS, capscale, adonis functions Oksanen et al., 2022). Through the CAP ranking of the environmental variables in line with their total contribution to inertia, including inertia co-explained with other variables, we evaluated the drivers of the variations in species composition in the "dieback" and "salvage" subsets. We also assessed the range of dissimilarity values within each dieback category in each country (vegan R-package, anosim function).

5.3 Results

Our final dataset comprised 16,075 specimens of 393 saproxylic beetle species belonging to 50 families in the Pyrenees and 3,470 specimens of 230 saproxylic beetle species belonging to 40 families in Bavaria.

5.3.1 Effects of forest dieback and salvage logging on stand metrics

Overall, forest dieback induced sharper environmental effects in Bavarian spruce than in Pyrenean silver fir forests, especially on the deadwood component but also on stand structure and TreMs. As expected, forest dieback led to a significant decrease in the basal area of living trees in both silver fir and spruce forests, and a parallel increase in various deadwood-related parameters: basal area of dead trees, lying deadwood volume (0.3-ha-scale), total deadwood volume and, to a lesser extent, deadwood diversity (0.3-ha-scale), and density of large snags and, to a lesser extent, of large logs (1-ha-scale; Fig. 5.3). In addition, declining spruce forests showed a significant increase in standing deadwood volume (0.3-ha-scale), relative basal area of dead trees, density of fungus-bearing trees and canopy openness, with a decrease in the density of saproxylic microhabitat-bearing trees and cavity-bearing trees, in particular (Fig. 5.3).

Salvage logging in Norway spruce declining stands had significant impacts on stand metrics. Even though it did not affect canopy openness, it did reduce total deadwood volume, lying deadwood volume (0.3-ha-scale) and the density of saproxylic microhabitat-bearing trees in both silver fir and spruce forests (Fig. 5.3). On the whole, salvage logging caused stronger differences with disturbed unharvested stands in spruce forests than in silver fir forests, where it generally had no significant impact (Fig. 5.3). In spruce forests, salvage logging reduced the density of large snags by 91%, large logs by 87%, standing deadwood volume by 95%, deadwood diversity by 56%, density of fungus-bearing trees by 95% and relative basal area of dead trees by 91% compared with unharvested declining plots (Fig. 5.3).

5.3.2 Effect of forest dieback and salvage logging on species richness, abundance and traits

Saproxylic beetle community metrics responded to forest dieback more strongly in the Bavarian spruce plots than in the Pyrenean silver fir plots (Fig. 5.3). Moreover, significant responses were distinct, and sometimes, the effects were even opposite between the two regions. The only unequivocal response we observed in both spruce and silver fir dieback plots was the lack of significant variations in the abundance and richness of xylophagous and xylofungicolous beetles among dieback classes (Fig. 5.4). With spruce dieback, red-listed, cavicolous, flower-visiting or zoophagous species had a higher abundance and

richness in declining than in healthy stands (Fig. 5.4). Conversely, forest dieback led to a decrease in the abundance and richness of zoophagous species in silver fir forests (Fig. 5.4).

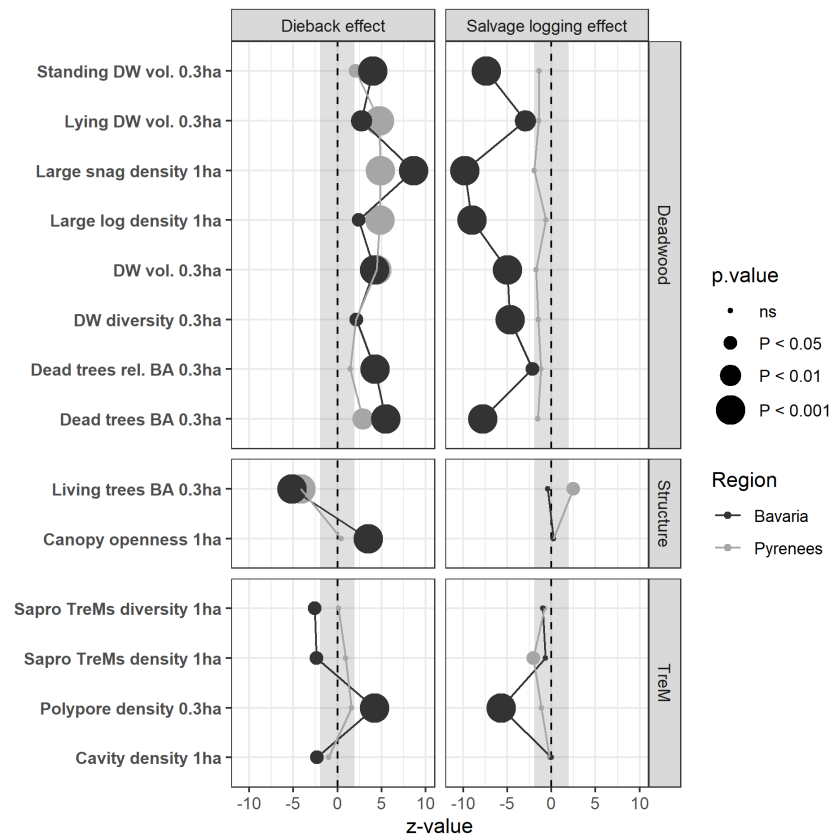


Figure 5.3 – Response of local forest stand features (deadwood, stand structure and tree-related microhabitats) to tree dieback (left panels) and salvage logging (right panels) in the Bavarian spruce forests (black) and in the Pyrenean silver fir forests (grey). Circles indicate effect significance and their diameter varies with p-value (lines between points are for visual purposes only); shaded areas indicate the range of non-significant values (z-values: ± 2.0).

Regarding deadwood niche characteristics, declining spruce stands hosted assemblages with higher mean-diameter trait values than did healthy stands: beetle species assemblages sampled in declining spruce stands were on average associated to larger deadwood (Fig. 5.4). The increasing mean and decreasing dispersion of the decay trait in declining spruce stands indicate that beetle assemblages occurring on these declining plots were mostly composed of species associated to more fully decayed deadwood (Fig. 5.4). The increase in mean and dispersion of the canopy trait in declining spruce stands indicates that both open-canopy and closed-canopy preferring species occurred on more declining plots, but that assemblages were on average associated to more closed-canopy conditions (Fig. 5.4). The decrease in canopy trait diversity for silver fir stands means that a narrower range of species in terms of canopy preferences occurred on the declining plots (Fig. 5.4).

Overall, the effects of both dieback and salvage logging practices on community metrics were stronger in the spruce than in the silver fir plots (Fig. 5.4). Abundance and richness of cavicolous species, richness of red-listed species and of xylofungicolous species, and mean diameter trait decreased and abundance of flower-visiting or zoophagous species increased in the salvage-logged spruce plots (Fig. 5.4). Contrary to expectations, the abundance of conifer-associated xylophagous beetles did not significantly decrease in the salvaged-logged spruce plots compared to unharvested declining plots, and it even increased in

the silver fir plots (Fig. 5.4). Finally, in the silver fir plots, the abundance of xylofungicolous species increased with salvage logging (Fig. 5.4).

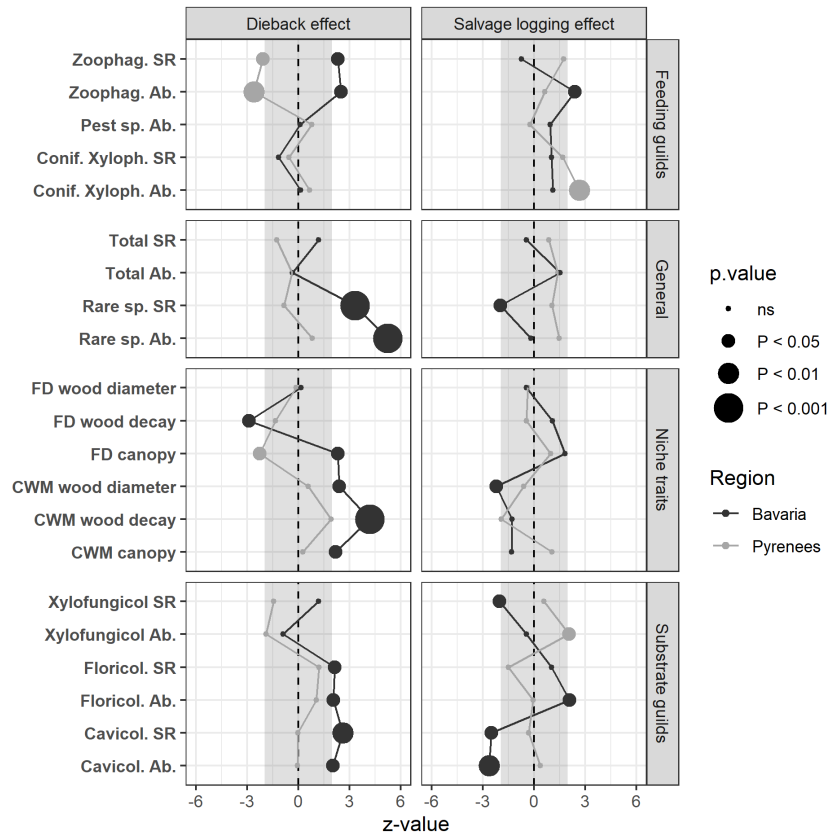


Figure 5.4 – Response of local saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics) to tree dieback (left panels) and salvage logging (right panels) in Bavarian spruce forests (black) and in Pyrenean silver fir forests (grey). Circles indicate effect significance and their diameter varies with p-value (lines between points are for visual purposes only); shaded areas indicate the range of non-significant values (z-values: ± 2.0).

5.3.3 Effects of forest dieback and salvage logging on assemblage composition

Effect of forest dieback on assemblage composition

Canonical Analysis of Principal coordinates (CAP) showed that the species composition of the saproxylic beetle assemblages was greatly modified by dieback in spruce (Fig. S5.3) but not in silver fir stands (Fig. S5.2). The silver fir CAP (Fig. 5.5) indicated that variations in species composition were only influenced by the dominant geographic site effect (Aure or Sault; Fig. 5.5 and S5.2). However, significant environmental drivers associated to tree dieback were detected in the spruce dataset. Among the local forest stand features, basal area of living trees, but also openness and density of large snags contributed the most to inertia (Fig. 5.5). To a lesser extent, basal area of dead trees, TreM density, total volume of deadwood and density of large logs also significantly contributed to variations in assemblage composition. Within-class dissimilarity in unharvested declining plots was not (spruce forests) or only slightly and non-significantly (silver fir forests) higher than in healthy plots (Fig. 5.6).

Effect of salvage logging practices on assemblage composition

Saproxylic beetle species composition was significantly modified by salvage logging, though to a lesser extent than by dieback, in spruce (Fig. S5.3) but not in silver fir forests (Fig. 5.5 and S5.2). The environmental drivers of species composition associated to salvage logging were quite close to the variables related to dieback. Whereas variations in saproxylic beetle composition were only influenced by a strong geographic site effect in the silver fir forests, they were governed by the prevailing effect of canopy openness, and driven, to a lesser extent, by TreM density, deadwood diversity, basal area of living trees and density of large logs and large snags in the spruce forests (Fig. 5.5). Within-class dissimilarity in unharvested declining plots was significantly (silver fir forests) or slightly but non-significantly (spruce forests) higher than in the salvaged plots (Fig. 5.6).

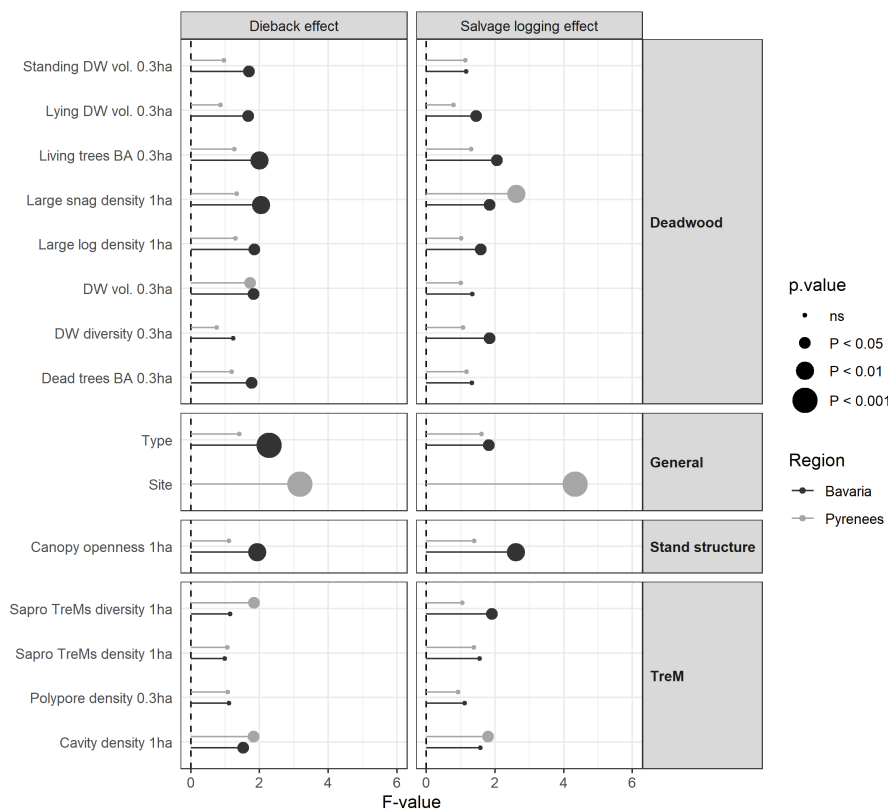


Figure 5.5 – Environmental drivers of variations in saproxylic beetle species composition, associated to tree dieback or salvage logging effects in Bavarian spruce forests (black) and in Pyrenean silver fir forests (grey). Effects of local stand features (deadwood, stand structure and tree-related microhabitats) tested with Canonical Analysis of Principal coordinates based on Bray-Curtis distance matrices: total inertia explained by each variable including inertia co-explained with other variables (bottom panel). Circles indicate effect significance and their diameter varies with p-value (100-run permutation tests).

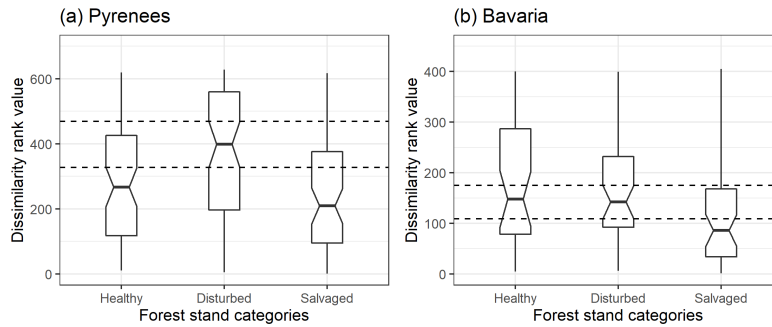


Figure 5.6 – ANOSIM plots showing the dissimilarity among beetle assemblages within the given forest stand categories in the Pyrenees (left) and in Bavaria (right). The bold horizontal bar in the box indicates the median; the bottom of the box indicates the 25th percentile; the top of the box indicates the 75th percentile and the extreme data points are marked by whiskers. Notches are used to differentiate group medians: if the notches for two boxes do not overlap, this is strong evidence that two medians differ (Chambers *et al.*, 2018). Dotted lines indicate lower and upper notches from the disturbed category for comparison with the healthy and salvaged categories.

5.3.4 Are the effects associated to forest dieback still significant after salvage logging operations?

Considering only the environmental variables that were both significant and included in the best models on community metrics, we detected many more effects of stand features associated to dieback effects (from healthy to declining) in the spruce than silver fir forests.

Overall, the metrics describing deadwood and stand structure had far stronger effects on saproxylic beetle assemblages than did TreMs (Tabs. 5.3 and 5.4).

In the spruce forests, the volume of standing deadwood was the most significant variable for saproxylic beetle communities with positive effects on abundance and species richness for all species, xylofungicolous, flower-visitor, zoophagous or red-listed species, but not for conifer-associated xylophagous species (Tab. 5.4). Cavicolous species positively responded to an increase in standing deadwood volume, both in abundance and richness (Tab. 5.4). Furthermore, the richness of all species and flower-visiting species increased with the density of large logs in the spruce forests (Tab. 5.4). In the silver fir stands, increasing canopy openness led to higher abundance for all species, as well as to higher abundance and richness for flower-visiting species (Tab. 5.3). The abundance of xylofungicolous species in the silver fir forests was positively affected by the basal area of living trees (Tab. 5.3).

Furthermore, several negative environmental effects associated to dieback were detected: there were slightly negative effects of lying deadwood diversity on the abundance of all species and xylofungicolous species in spruce forests (Tab. 5.4), and of zoophagous species in silver fir forests (Tab. 5.3); and a slight negative effect of the local density of TreMs on the abundance of red-listed species (in spruce forests; Tab. 5.4).

The vast majority (79% in the spruce stands, Tab. 5.4; 100% in the silver fir stands, Tab. 5.3) of these significant environmental effects associated to dieback were no longer significant after salvaged plots were included in the analysed data, i.e. in the subset merging salvaged and unharvested declining plots.

5.4 Discussion

5.4.1 Overall natural and anthropogenic disturbance effects

In both of the forest contexts in our study, dieback provided a biological legacy through an increase in deadwood resources (Fig. 5.3); however, the increase in deadwood resources was much greater in the spruce forests. In addition, in the spruce forests, dieback provided a structural legacy through an increase in canopy openness (Fig. 5.3). As a result, assemblage species composition was more strongly modified by dieback in the spruce than in the silver fir forests (Figs. 5.2, S5.2 and S5.3). Nonetheless, despite this increase in resources, and in contrast to other studies (Müller et al., 2010; Thom and Seidl, 2016), neither type of forest gained in total abundance or species richness after disturbance, compared to healthy stands. In our analyses, we did not take into account geographical features such as altitude or slope orientation, in addition to stand features. However lower altitudes or sun exposed slopes could significantly affect insect communities and their response to environmental changes. Nonetheless, all our study plots remain in the montane context (min: 660 m; max: 1560 m).

Table 5.3 – Effects of stand features (deadwood, stand structure and tree-related microhabitats) associated to dieback and salvage logging effects in **Pyrenean silver fir forests** on saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics). Effects were tested with generalized linear mixed models (using "site" as a random variable). The variables involved in the best model of dieback effects (left panel) were assessed (direction and significance) in the models of salvage-logging effects (right panel). "Neg. binom." is the negative binomial probability distribution; "poisson" is the Poisson distribution"; "linear" is the Gaussian distribution.

Response variable	Probability distribution	Disturbed + Healthy		Disturbed + Salvaged	
		Best model	Estimate (β) \pm se	Estimate (β) \pm se	Estimate (β) \pm se
General guilds					
Total Ab.	Neg. binom.	Canopy openness 1 ha	0.28** \pm 0.1	0.14 ^{ns} \pm 0.14	
Total SR	Neg. binom.	Null model			
Rare sp. Ab.	Neg. binom.	Large log density 1 ha	0.34* \pm 0.16	0.1 ^{ns} \pm 0.35	
Rare sp. SR	Poisson	Null model			
Substrate guilds					
Xylofungicol. Ab.	Neg. binom.	Living trees BA 0.3 ha	0.31** \pm 0.1	0.1 ^{ns} \pm 0.11	
Xylofungicol. SR	Neg. binom.	Null model			
Cavicol. Ab.	Neg. binom.	Null model			
Cavicol. SR	Poisson	Log standing DW vol. 0.3 ha	-0.15 ^{ns} \pm 0.09	0.06 ^{ns} \pm 0.08	
Adult feeding guilds					
Floricol. Ab.	Neg. binom.	Canopy openness 1 ha	0.27* \pm 0.1	0.15 ^{ns} \pm 0.13	
Floricol. SR	Neg. binom.	Canopy openness 1 ha	0.23* \pm 0.09	0.18 ^{ns} \pm 0.09	
		Sapro TreM density 0.3 ha	0.14 ^{ns} \pm 0.09	0.17* \pm 0.08	
Larva feeding guilds					
Zoophag. Ab.	Neg. binom.	Lying DW diversity 0.3 ha	-0.25* \pm 0.1	-0.15 ^{ns} \pm 0.11	
Zoophag. SR	Neg. binom.	Log standing DW vol. 0.3 ha	-0.11 ^{ns} \pm 0.07	0.11 ^{ns} \pm 0.09	
Conif. Xyloph. Ab.	Neg. binom.	Canopy openness 1 ha	0.41 ^{ns} \pm 0.2	-0.08 ^{ns} \pm 0.3	
Conif. Xyloph. SR	Poisson	Canopy openness 1 ha	0.16 ^{ns} \pm 0.08	0.14 ^{ns} \pm 0.08	
Pest sp. Ab.	Neg. binom.	Canopy openness 1 ha	0.57* \pm 0.26	0.38 ^{ns} \pm 0.27	

Salvage logging caused significant contrasts in dieback effects for stand and community metrics between the spruce and silver fir plots. Globally, salvage logging modified assemblage species composition in the spruce forests only, not in the silver fir forests. This modification was less than for dieback. Unlike the overall negative impact of salvage logging on saproxylic beetle richness found in the

meta-analysis by Thorn et al. (2018a), in our study salvage logging had non-significant, or only slightly significant, effects on saproxylic beetles (Fig. 5.4).

5.4.2 Saproxylic beetles were affected by habitat/resource changes induced by forest die-back

Effects of changes in habitat/resource quantity

In the spruce plots, saproxylic beetles responded positively to the large increase in deadwood in the declining stands, as shown by an asymptotic concave function model (Fig. 5.7 a and b), in accordance with the "*Species-Resource Relationship*" (SRR) concept (Godeau et al., 2020). The "*species-energy hypothesis*" may be the underlying driver here (Seibold et al., 2016). Forest dieback resulted in higher amounts of large snags and logs, which are known to be key factors for saproxylic beetles (Bouget et al., 2014a). The highly positive impact of increasing dieback on red-listed species, probably driven by the increase in volume of large deadwood and especially snags (Tab. 5.4), should be underlined. According to our trait database, the rare or red-listed species captured in our study were, on average, more closely associated to larger deadwood than were the common species (Fig. S5.7); this confirms the importance of large deadwood pieces for insect diversity conservation. Accordingly, saproxylic species in declining spruce stands had a preference for larger deadwood than in healthy stands. Previous studies had already shown the importance of large deadwood for saproxylic beetles (Bouget et al., 2012, 2014a; Brin et al., 2011). In addition, for degree of deadwood decay, the mean trait increased while the functional diversity decreased with dieback, indicating that increasing forest dieback favoured a specialist community associated to well-decayed deadwood pieces. These results for diameter and decay niche traits are in line with Gossner et al. (2013), who found beetle assemblages with a higher demand for large-diameter and highly-decayed deadwood in forests where large amounts of deadwood had accumulated.

Table 5.4 – Effects of stand features (deadwood, stand structure and tree-related microhabitats) associated to dieback and salvage logging effects in **Bavarian Norway spruce forests** on saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics). Effects were tested with generalized and general linear models. The variables involved in the best model of dieback effects (left panel) were assessed (direction and significance) in the models of salvage-logging effects (right panel). "Neg. binom." is the negative binomial probability distribution; "linear" is the Gaussian distribution.

Response variable	Probability distribution	Disturbed + Healthy		Disturbed + Salvaged
		Best model	Estimate (β) \pm se	Estimate (β) \pm se
General guilds				
Total Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	0.49*** \pm 0.13	-0.08 ^{ns} \pm 0.13
		Lying DW diversity 0.3 ha	-0.31* \pm 0.12	0.19 ^{ns} \pm 0.12
Total SR.	Neg. binom.	Log standing DW vol. 0.3 ha	0.29*** \pm 0.10	0.06 ^{ns} \pm 0.08
		Large log density 1 ha	0.21* \pm 0.09	0.12 ^{ns} \pm 0.07
Red-listed sp. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	1.43*** \pm 0.42	-0.26 ^{ns} \pm 0.21
		Sapro TreM density 0.3 ha	-0.42* \pm 0.16	0.09 ^{ns} \pm 0.23
Red-listed sp. SR	Neg. binom.	Log standing DW vol. 0.3 ha	0.96*** \pm 0.25	0.48** \pm 0.15
Substrate guilds				
Xylofungicol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	0.7** \pm 0.22	0.18 ^{ns} \pm 0.15
		Lying DW diversity 0.3 ha	-0.6** \pm 0.19	-0.09 ^{ns} \pm 0.15
Xylofungicol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	0.37** \pm 0.13	0.08 ^{ns} \pm 0.14
Cavicol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	0.69** \pm 0.23	0.57** \pm 0.17
Cavicol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	0.41* \pm 0.19	0.13 ^{ns} \pm 0.19
Adult feeding guilds				
Floricol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	0.74** \pm 0.23	-0.22 ^{ns} \pm 0.16
Floricol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	0.46** \pm 0.16	-0.07 ^{ns} \pm 0.08
		Large log density 1 ha	0.28* \pm 0.13	-0.005 ^{ns} \pm 0.09
Larva feeding guilds				
Zoophag. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	0.66*** \pm 0.13	-0.16 ^{ns} \pm 0.12
		Lying DW diversity 0.3 ha	0.2 ^{ns} \pm 0.1	0.08 ^{ns} \pm 0.15
Zoophag. SR	Neg. binom.	Log standing DW vol. 0.3 ha	0.42*** \pm 0.11	0.11 ^{ns} \pm 0.09
Conif. Xyloph. Ab.	Neg. binom.	Sapro TreM density 0.3 ha	-0.56* \pm 0.26	-0.73* \pm 0.29
Conif. Xyloph. SR	Neg. binom.	Null model		
Pest sp. Ab.	Neg. binom.	Sapro TreM density 1 ha	-0.58* \pm 0.27	-0.77* \pm 0.3

Unsurprisingly, among the environmental drivers associated to dieback effects, increasing snag density had a strong and significant influence on univariate community metrics (Tab. 5.4) and assemblage composition in spruce forests (Fig. 5.5). According to the literature, snags (and even more so, large snags) decline drastically in managed forests (Ekbom et al., 2006), even though they are essential for rare or red-listed species conservation (Bouget et al., 2012, 2014a; Hammond et al., 2004; Kappes and Topp, 2004; Sverdrup-Thygeson and Ims, 2002).

The lack of response of the saproxylic beetle communities in the silver fir plots may be explained by the relatively low amount of deadwood generated by the drought-induced dieback, with levels remaining below critical threshold values (Müller and Bütler, 2010).

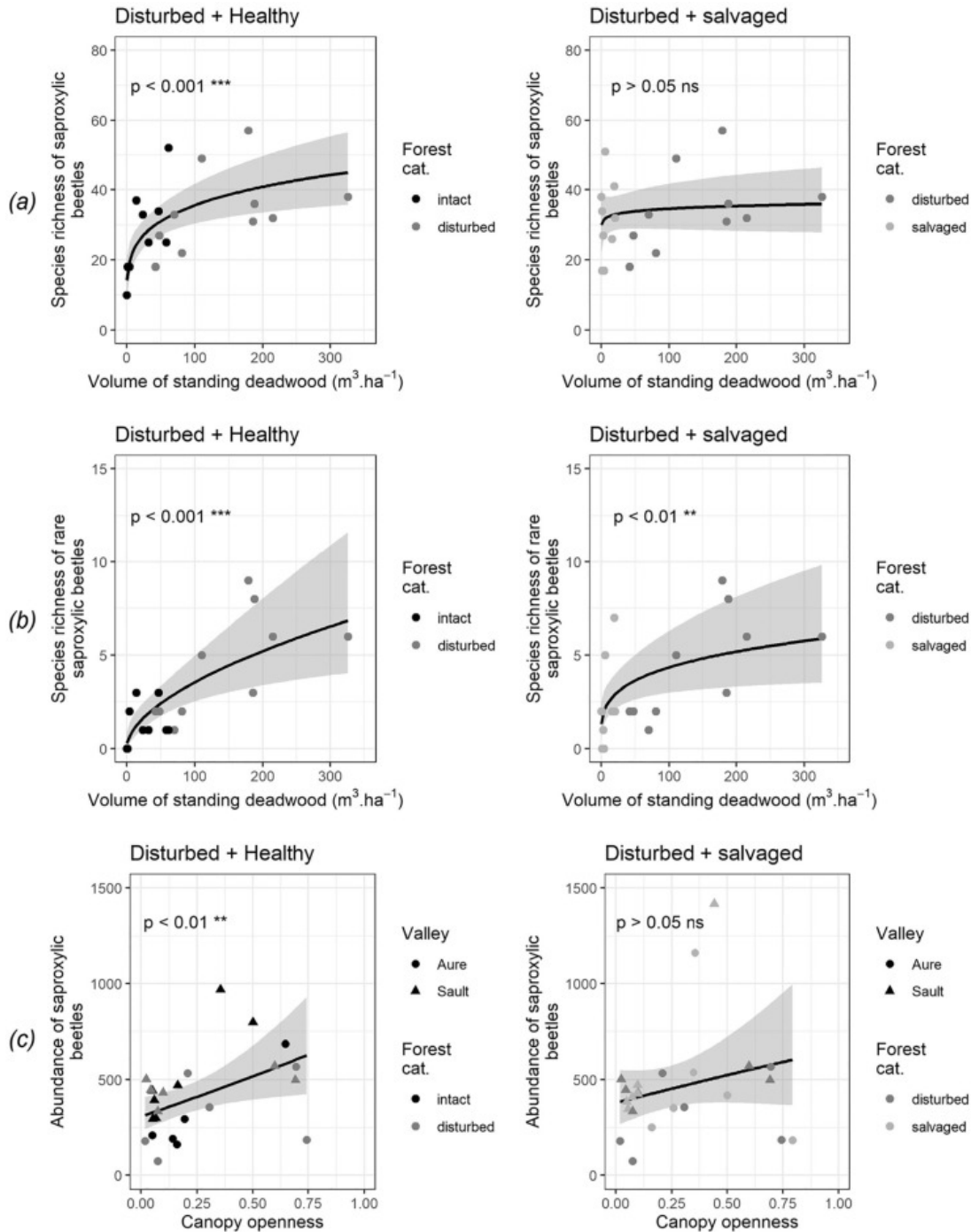


Figure 5.7 – Relationship between standing deadwood volume in Bavarian spruce forests and mean species richness of saproxylic beetles (a), or red-listed saproxylic beetles (b), and between canopy openness in Pyrenean silver fir forests and mean abundance of all saproxylic beetles (c). Left: disturbed and "intact" (or healthy) stands; Right: disturbed and salvaged stands. The black line is the regression curve from the negative binomial model (with a log-transformation of x) and the grey area indicates the 95% confident interval. "intact" = "healthy".

Effects of changes in habitat/resource heterogeneity

Habitat heterogeneity has several dimensions at the local scale. Firstly, higher canopy-openness values

indicates a finer-grain within-stand mosaic of closed-canopy and open-canopy patches. In our case study, canopy openness, which increased with stand dieback in the spruce stands, strongly drove assemblage composition and significantly fostered flower-visiting species (Fig. 5.5), and positively influenced several guilds of saproxylic beetles in the silver fir stands (Fig. 5.7 and Tab. 5.3). Similarly, Bouget et al. (2013) had already described potential interactions between an open-mosaic forest environment and saproxylic beetles. Secondly, substrate diversity, i.e. deadwood and TreM diversity, reflects the number of available niches. In our study, deadwood diversity increased in both declining spruce and silver fir stands, though less strongly than deadwood volume, whereas TreM diversity decreased (although not significantly in the silver fir context). In addition, deadwood diversity did not appear among the best variables influencing total species richness and abundance, as did deadwood volume. Nevertheless, (i) deadwood volume and diversity were highly correlated (Fig. S5.8), and (ii) total saproxylic beetle species richness, taken independently, responded positively to deadwood diversity in the spruce stands (Fig. S5.9). Therefore, habitat quantity and heterogeneity could possibly have had additive positive effects on saproxylic beetle species, in agreement with the "*habitat-heterogeneity hypothesis* underlying species coexistence (Seibold et al., 2016).

5.4.3 Salvage logging caused the loss of ecological relationships resulting from the dieback process

Most of the significant environmental effects on biodiversity associated with dieback were no longer significant after accounting for the salvaged plots in our study data (Tab. 5.3 and 5.4). Moreover, we measured a large depletion of deadwood resources in salvaged declining stands compared with declining unharvested stands in the spruce forests (an 86% decrease in total deadwood on average; Fig. 5.3). However, whereas saproxylic beetles positively responded to the additional dieback-induced deadwood in spruce stands (see 4.2; Fig. 5.7), they did not decrease in abundance or species richness subsequent to deadwood depletion (Fig. 5.4). Deadwood is one of the main biological legacies induced by forest dieback (Swanson et al., 2011) and we therefore expected its loss to affect the key group of saproxylic beetles. Extinction debt processes may explain the limited immediate deleterious effects of salvage harvests in our results (Kuussaari et al., 2009; Tilman et al., 1994). Indeed, saproxylic beetle species may initially survive the habitat loss following the harvesting, but then go extinct after a "*relaxation time*" determined by species life span and landscape mitigation processes related to neighbouring habitat patches and beetles dispersal abilities (Kuussaari et al., 2009).

Nevertheless, when comparing the declining unharvested plots to the salvaged declining plots, we measured several functionally consistent responses of the beetle community in the spruce forests:

- i we found a decrease in red-listed species richness parallel to a decreased mean diameter niche trait as a result of the decrease in large snags and large logs (Fig. 5.3 and 5.4);
- ii we found a decrease in the species richness of fungicolous beetles as a result of a decrease in the density of fungus-bearing trees (Fig. 5.3 and 5.4).

The negative consequences of salvage logging on red-listed species richness had already been highlighted by Thorn et al. (2014) in the same region, and was likely due to the decrease in snag density. Furthermore, on our spruce plots, cavicolous beetles declined in both abundance and richness parallel to the decrease in snag volume (Fig. 5.4 and Tab. 5.4). For zoophagous beetles, the significant increase in their abundance in our salvaged declining spruce stands was not consistent with a potential bottom-up effect of beetle decline on higher trophic levels within the saproxylic food web.

In line with a likely decrease in habitat heterogeneity caused by the salvage logging, as suggested by the consistently observed reduction in deadwood diversity in spruce stands, we detected an increase in within-class assemblage similarity in the salvaged declining plots compared to the unharvested declining plots (significant for silver fir but not for spruce stands; Fig. 5.6). Removing all of the biological

legacies inherited from the forest dieback during salvage logging would likely simplify the forest structure compared to declining unharvested stands. In agreement with our results, this could lead to reduced variability in species composition, i.e. community homogenisation (Cobb et al., 2007). It should be remembered, however, that the positive relationship between within-stand heterogeneity and local forest biodiversity has been empirically challenged (see above; Schall et al., 2018, despite the strong theoretical background supporting this relationship; Wilson, 2000).

In the Bavarian context, response patterns to salvage were clearer but it should be noticed that unharvested declining plots and salvaged plots not only differed by harvesting practices but also by a different time lag from the dieback-inducing event. Indeed, massive bark beetle outbreaks occurred in 2001 (± 5 years) in unharvested plots and in 2009 (± 4 years) in harvested plots, which could have amplified short-term effects of salvage harvests studied in 2016.

5.4.4 Contrasting responses of saproxylic beetle communities according to forest dieback context

Forest dieback and salvage logging induced much sharper and stronger effects on environmental and community metrics in the spruce than in the silver fir forests (Tab. 5.5 and Fig. S5.10). Whereas the species composition of saproxylic beetle assemblages was significantly affected by dieback and salvage logging in spruce stands, neither dieback nor salvage logging modified species composition in the silver fir forests. Potential limitations in our comparison of case studies should be reminded. The contrast between Bavaria and the French Pyrenees seems partly related to dieback "severity" (Figs. 5.2 and 5.7; Tab. 5.5). A simulation approach suggested that more severe disturbances have more positive impacts on biodiversity (Thom et al., 2017a). In the spruce stands, pest-induced dieback recently caused massive tree mortality over large landscape (Thorn et al., 2014), while in the silver fir stands, drought-induced dieback generated only small patches of dead trees (Camarero et al., 2011), even if recurrent droughts can result in significant long-term delayed mortality (Bréda et al., 2006). The spruce forests in our study naturally have a higher baseline level of deadwood than the silver fir forests (Tab. 5.5); in addition, they showed a stronger dieback-induced increase in deadwood and in canopy openness (Tab. 5.5). Moreover, even though spruce and silver fir are valuable species-rich host trees (Lemperiere and Marage, 2010; Müller et al., 2015), the regional species-pool in the Bavarian National Park landscape was possibly more likely to be enhanced by improved habitat conditions. Indeed, saproxylic beetles are known to respond to large-scale habitat effects (Gibb et al., 2006; Økland et al., 1996).

Table 5.5 – Some of the features characterising the two forest dieback processes in the study.

Features	Bavaria	Pyrenees
Dieback agent	Storm + bark beetle outbreak	Droughts
Tree species	<i>Picea abies</i>	<i>Abies alba</i>
Studied species proportion	77%	62%
Dieback severity	High-severity	Moderate-severity
Disturbance scale	Large	Large
Size of deadwood patches	Landscape scale	Local scale
Year of onset 2001	(± 5 years)	2003
Baseline deadwood level in healthy plots	60.2 m ³ .ha ⁻¹	23.4 m ³ .ha ⁻¹
Average deadwood accumulation caused by dieback	+212.3 m ³ .ha ⁻¹ (+353%)	+60.6 m ³ .ha ⁻¹ (+259%)
Decrease in living-tree basal area caused by dieback	-36.6 m ² .ha ⁻¹ (-86%)	-16.4 m ² .ha ⁻¹ (-42%)
Increase in canopy openness caused by dieback	+53%	+9.4%


5.5 Implications for forest management and future research

Saproxylic beetle species had contrasting responses to disturbance depending on the type of disturbance (drought-induced or pest-induced dieback and salvage logging). In Bavaria, they benefitted from the severe forest dieback caused by massive bark beetle outbreaks. Conversely, they did not significantly respond to the drought-induced forest dieback in the Pyrenees. Indeed, the local accumulation of deadwood in the French plots was insufficient to favour saproxylic biodiversity. Further research should consider the influence of (i) dieback level at the landscape scale on local and regional biodiversity, (ii) contrasting factors that trigger dieback, and (iii) dieback severity. Future investigations should also focus on the network design of retention patches of deadwood-rich areas in managed forest landscapes (Müller et al., 2010). Retaining biological legacies associated to forest dieback (such as large snags) could help to limit the negative impact of salvage logging on key habitat features and may therefore be a good addition to a biodiversity-friendly management approach.

5.6 Supplementary material

Supplementary materials for this chapter can be found in appendix C.

The living from the dead: changes in taxonomical and functional composition of saproxylic beetles communities following natural disturbances

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6.1 Introduction

Natural disturbances are key drivers of forest ecosystem composition, dynamics and processes. They directly affect forest organisms, their local environmental conditions and landscape heterogeneity (Pickett and White, 1985; Thom and Seidl, 2016; Viljur et al., 2022). Climate change affects the intensity, severity, frequency and/or spatial extent of natural disturbances (i.e. their regime; Seidl et al., 2017; Turner, 2010). For example, droughts are expected to become more intense, prolonged, frequent and widespread in Europe (Samaniego et al., 2018), and droughts are now considered as a major threat for forest ecosystems worldwide (Batllori et al., 2020; Senf and Seidl, 2021b).

Severe disturbances can affect tree condition, with immediate and/or delayed impacts on their survival, over local to landscape scales (Allen et al., 2015; McDowell et al., 2020; Senf et al., 2018, 2020). This can result in more or less gradual losses of tree vigour and tree death, sometimes over large spatial scales, referred as forest diebacks and/or declines. Through these dieback and decline processes, natural disturbances can abruptly or progressively increase the amount of dead wood, alter the provision of tree-related microhabitats (TreMs; Larrieu et al., 2018) like trunk cavities, perched dead wood, loose bark etc., generally referred to as disturbance legacies (Franklin et al., 2000; Johnstone et al., 2016; Swanson et al., 2011). Increasing crown dieback during the decline process also affect forest microclimates and the provision of ground-related resources. This can consequently markedly reshape forest communities with deleterious effects on some trophic and/or habitat guilds, but also by creating colonization opportunities for some other guilds (Cours et al., 2021; Kozák et al., 2021; Thorn et al., 2017; Viljur et al., 2022; Waldron et al., 2013).

Arthropods encompass very diverse communities, that occupy a wide range of niches in ecosystems around the world. They are of major interest in the web of species interactions in ecosystems and

are therefore of great ecological importance (Wermelinger, 2021). The current decline of arthropod communities (Hallmann et al., 2017; Lister and Garcia, 2018; Seibold et al., 2019; Van Klink et al., 2020), and their ecological importance make it all the more necessary to study their responses to environmental change. Among forest arthropods, saproxylic beetles (i.e. beetles related to dead or decaying wood for at least part of their life cycle) play a prominent role in ecosystem functioning as they contribute to the wood decay processes. They are, however, strongly affected by the overall reduction in the amount and diversity of dead wood in managed forests (Grove, 2002; Müller et al., 2013; Siitonen, 2001; Stokland et al., 2012). Because of their expected response to increased dead wood resources and changes in TreMs composition and abundance, and their well-known biology (Bouget et al., 2019), saproxylic beetles are a very appropriate guild to study the response of biodiversity to natural disturbances (see e.g. Beudert et al., 2015; Cours et al., 2022; Kozák et al., 2021; Tello et al., 2022).

To our knowledge, previous studies on the response of saproxylic beetles to natural disturbances have focused separately on α -diversity (i.e. local community response) or β -diversity, either along a gradient of dieback (i.e. the compositional response between dieback classes), or among plots within a dieback class (i.e. response of species distribution within a same dieback class). These studies also considered either taxonomic diversity or functional diversity. Overall, previous studies showed that both taxonomic and functional α -diversity of saproxylic beetles benefit from natural disturbances due to an increase in dead wood resources (Beudert et al., 2015; Cours et al., 2021; Viljur et al., 2022; Wermelinger et al., 2002), even if these positive responses could be scale dependent (Cours et al., 2022; Viljur et al., 2022). In parallel β -diversity across a gradient of dieback showed significant, but non linear, responses of taxonomic compositions depending on disturbance occurrence and severity (Cours et al., 2021; Georgiev et al., 2022; Kortmann et al., 2022; Sire et al., 2022; Winter et al., 2017). Moreover, the β -diversity within dieback classes can be reduced between intact and disturbed forests (e.g., for windstorms Georgiev et al., 2022). Nonetheless, there is few studies on mechanisms regulating changes in β -diversity e.g., through β -diversity partitioning.

In our study, we sought to better understand the α - and β -diversity responses of both the taxonomic and functional compositions of saproxylic beetles to natural disturbances through the changes in abiotic conditions in three different contexts. Taxonomic diversity pertains the selection of species diversity and composition, while functional diversity pertains the selection of species traits by environmental gradients. We expected (i) an increase in α -diversity in disturbed areas due to the changes in abiotic conditions while, (ii) the overall resource increase would lead to a reduced β -diversity among plots, as a result of saproxylic beetle generalisation over disturbed areas (Fig. 6.1). Furthermore, we partitioned the β -diversity within-dieback classes in a replacement (or turnover) and richness (or gain/loss) components (Baselga, 2010; Cardoso et al., 2014; Carvalho and Cardoso, 2020). The replacement component pertains to the replacement of a species or a trait by another between plots while richness component pertains to the differences (gain/loss) in species or trait richness between plots. Due to the generalisation of saproxylic beetles in highly disturbed landscapes, (iii) we expected higher replacement component and a lower richness component along the dieback gradient. Moreover, due to the direct selection of traits by environmental changes due to forest dieback, we expected greater responses by functional than taxonomic diversity and composition.

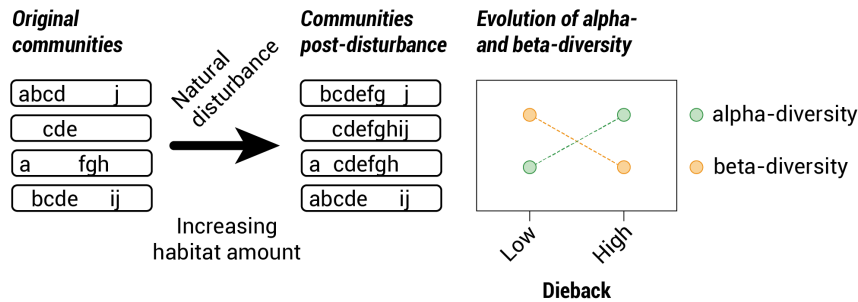


Figure 6.1 – Schematic representation of our hypothesis. In response to the increase amount of resource availability due to natural disturbance, we hypothesized an increase in alpha-diversity followed by a decrease in beta-diversity, due to the generalisation of the saproxylic beetle guild across plots.

6.2 Materials and methods

6.2.1 Sampling design

Our study was conducted in three different forest contexts: two in France (the Silver fir-dominated forests (*Abies alba* Mill.) in French Pyrenees, hereafter in text "fir forests", and the oak-dominated forests (mix of *Quercus petraea* (Matt) Liebl. and *Quercus robur* L.) in Loire valley, hereafter in text "oak forests"), and one in Germany (the Norway spruce-dominated forests (*Picea abies* (L.) H. Karst) in Bavaria, hereafter in text "spruce forests"; Fig. 6.2). Along an empiric gradient of forest dieback, we selected 43 study plots in fir forests (21 in Aure valley (Central Pyrenees; 854 to 1570 m a.s.l., 1298 m on average; 42°51'46.8"N 0°36'08.9"E) and 22 on Sault plateau (Eastern Pyrenees; 705 to 1557.3 m a.s.l., 1029 m on average; 42°50'58.7"N 2°00'41.3"E)), 15 plots in oak forests (6 in Orleans forest (107 to 174 m a.s.l.; 48°00'28"N 2°09'39"E) and 9 in Vierzon forest (120 to 190 m a.s.l.; 47°15'53.9"N 2°05'55.4"E)), and 19 plots in spruce forests (660 to 1352 m a.s.l.; 49°1'24.96"N 13°38'5.222"E; Fig. 6.2). In fir and oak forests, plots were set up in managed forests and the forests around were also predominantly managed while, in spruce forests, plots were set up in the core zone of Bavarian Forest National Park characterized by a generalized benign neglect strategy without any human intervention, as part of the BIOKLIM project (Bässler et al., 2009; Thorn et al., 2017). Decline in fir and oak forests were mainly the result of drought events (the drought of 2003 being a major event in the occurrence of these diebacks), which mainly resulted in patch dynamics (Andrew et al., 2016; Sallé et al., 2020). In spruce forests, the dieback studied was the result of several successions of compounded windstorms and bark beetle outbreaks, which mainly resulted in stand-replacing dynamics (Thorn et al., 2017). No salvage logging occurred in both fir and spruce forests, while the most valuable oak trees were regularly harvested during the decline process, which reduced the amount of dead wood in these forests (Fig. 6.3).

6.2.2 Environmental conditions

Firstly, in each study plot, we assessed the forest dieback severity. In fir and oak forests, we based the assessment on the observation of the 20 nearest co-dominant and dominant trees of the plot centre. This observation result in a notation of tree health using their crown architecture, in reference to a fully alive tree crown of the same species (ARCHI protocol; Drénou et al., 2013). These observations lead to the calculation of a standardized index of dieback, from 0 when all the 20 trees were fully alive, to 1 when all the 20 trees were all dead. For several multivariate analysis, we divided the standardized index in three classes i.e., "low", "mid" and "high" dieback. In parallel, in spruce forests, we only used two classes of dieback i.e., "low" and "high" since we do not measured the standardized index in this context.

For the dendometric characterisation of each plot, we implemented a relascope sampling protocol

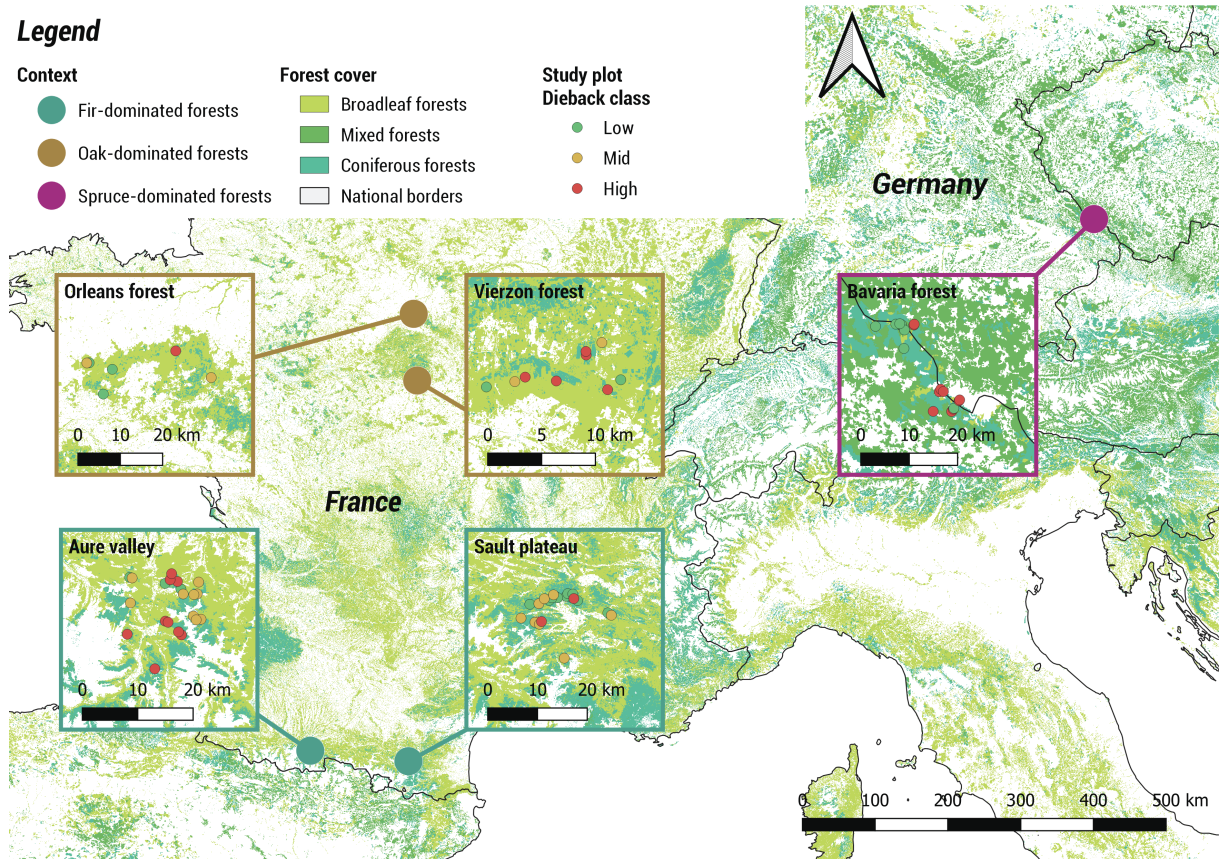


Figure 6.2 – Map of the study plots and of the different study contexts.

using Bitterlich relascope with 1/50 ratio (Bitterlich, 1984). We recorded the type (i.e. living tree, standing dead tree and lying dead wood), the tree species, the diameter (at breast height on living trees and standing dead trees higher than 4 m, and at mid-height on standing trees lower than 4 m and on lying dead wood), and the decay stage for dead wood (from 1 = fresh dead wood with full cover of bark, to 4 = soft wood with no more remaining barks). In addition, for each tree within plot, we recorded the tree-related microhabitats (TreMs) on living and standing dead trees, based on the 47 types describes by Larrieu et al. (2018). Mean plot area was approximately of 0.3 ha and depended on tree diameter and their location from the center. Finally, we convert plot's data into 1ha densities by allocating to every measured trees and dead wood pieces, the coefficient N_d (Eq. 6.1; Pardé and Bouchon, 1988). Field data were collected in 2017 in the fir and spruce forests, and in 2020 in oak forests.

$$N_d = \pi \times 10^8 \times \left(\frac{\arctan(1/50)}{(\pi \times dbh)} \right)^2 \quad (6.1)$$

In parallel, we used eco-morphological traits related to each woody element (i.e. living trees and dead wood) and TreM, to described environmental change and abiotic filters. For woody elements, we directly used field measurements i.e., type of substrate ¹, decay stage ², and diameter.

In addition, we used a list of five eco-morphological traits characterizing each TreM found on field: (i) type of substrate bearing the TreM, (ii) vertical position in tree, (iii) wetness, (iv) life span, and (v)

1. As an ordinal scale: 1 = "lying dead wood", 2 = "standing dead wood", 3 = "living trees"

2. From 0 = "living biomass", to 4 = "very soft wood out of bark"

ontogenesis. We used the same method than Gossner et al. (2013): each trait was categorized (e.g., vertical position in tree = tree base, trunk and crown) and for each TreM, we allocated a degree of occurrence in each category based on expert opinion (for further information, please see section 4).

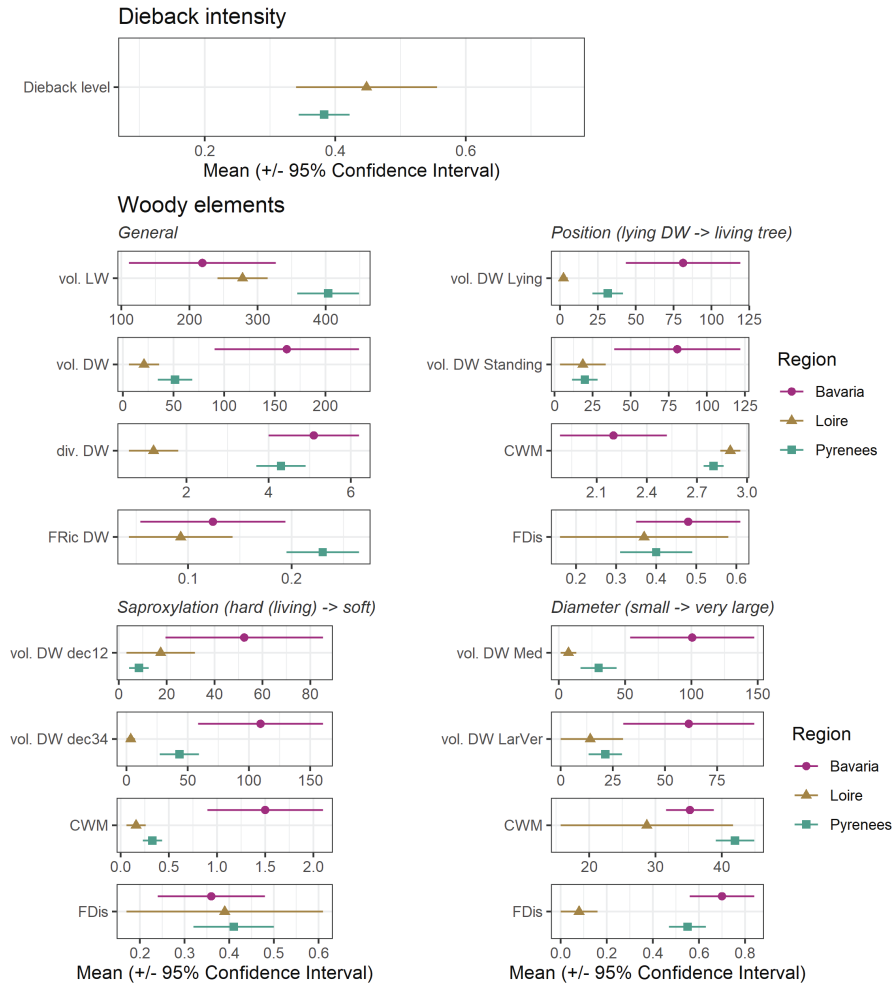


Figure 6.3 – Overview of predictors used in our study for dieback intensity and woody elements in each study region. Forest dieback was categorized in spruce forests, so it is absent from "dieback intensity" panel.

6.2.3 Beetle sampling, identification and characterization

We sampled saproxylic beetles using different type of traps in each study context. In fir and spruce forests, we used flight-interception traps (©Polytrap). They consisted in crossed pair of transparent plastic panes (40 × 60 cm) above a funnel conducting into a container filled with an unbaited preservative (50% propylene glycol and 50% water with a drop of detergent). There were two interception-traps in fir forests, each at least 20 m from the other, placed around the centre of each study plot (Cours et al., 2022), while there was only one interception-trap in spruce forest, placed at the center of each study plot (Cours et al., 2021). The traps were suspended roughly 1.5 m above the ground and were sampled every month from mid-May to mid-September 2016 in spruce forests and 2017 in fir forests. In oak forests, we used a combination of two types of traps in each plot, two green multi-funnel traps (©Lindgren) to sample *Agrilus* species (Sallé et al., 2020) and one black multi-funnel trap baited with volatiles to sample saproxylic beetles. As in fir and spruce forests, collectors were filled with an unbaited preservative (50%

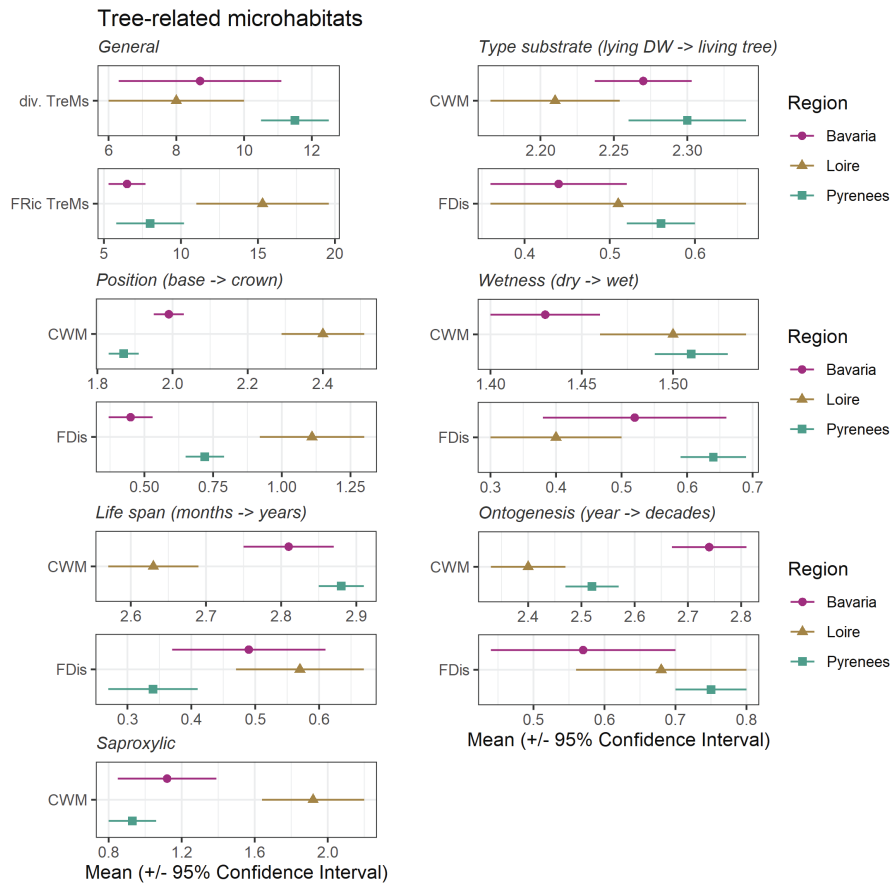


Figure 6.4 – Overview of predictors used in our study for tree-related microhabitats in each study region.

propylene glycol and 50% water with a drop of detergent). Each trap was installed in a separate tree at least 50 m from each other. These traps were suspended in the tree canopy, 15 m above the ground. The traps were sampled every month from mid-May to the end of August 2020. All the captured saproxylic beetles were identified at the highest possible taxonomic level (i.e., 87% of abundance at the species level, 1% at the genus level and 12% at the family level). We retained the genera in which at least 100% of regional species are known to be saproxylic, and families in which at least 75% of regional species are known to be saproxylic (Bouget et al., 2019). Since we were not able to identify most of Staphylinidae species, we excluded them from the data sets.

We characterized each saproxylic beetle species by five quantitative traits: (i) the preference in dead wood diameter and (ii) stage of decay, (iii) the preference in canopy closure, (iv) the mean body size and (v) the rarity. The three first indices were based on species occurrence data, i.e. class of dead wood diameter and stage of decay, and canopy cover in which species were recorded. We mainly reused data from Gossner et al. (2013) and Janssen et al. (2017). Mean body size was based on direct measurements from the FRISBEE database (Bouget et al., 2019). Rarity was defined using the patrimonial indicator (IP) related to the biogeographic rarity, an ordinal scale from 1 (i.e. common species) to 4 (i.e. very rare species known from only five localities in France) (Bouget et al., 2019; Brustel, 2001). For the sake of convenience, we used patrimonial indicator from French species on the German data set.

6.2.4 Statistical analysis

Data analysis was conducted with R software 4.1.2 (R Core Team, 2022). Our work was divided into two stages: the first part was based on structural equation modelling (SEM), while the second was based

on the study of the taxonomic and functional composition. In contexts where we used several traps for a same study plot (i.e. the fir and oak forests), we pooled them for the analysis.

Univariate analysis

We calculated the different predictors and response variables. We used the quantitative eco-morphological traits from woody elements and TreMs to compute community weighted means (CWM) and functional dispersion (FDis) for each of them, as predictors, using FD R-package (Laliberté et al., 2014; Figs. 6.3 and 6.4). We also calculated the functional richness (FRic) of dead wood and TreMs based on the eco-morphological traits and the FD R-package (Laliberté et al., 2014). We excluded living trees from this last analysis. In parallel, for saproxylic beetles, we used the plot \times community matrices and the quantitative trait database (i.e. the preference in dead wood diameter and stage of decay, and in canopy closure, the mean body size and the rarity) to produce functional hypervolumes defining the functional spaces occupied by communities in each study plot (Mammola and Cardoso, 2020). With these hypervolumes, we calculated functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve), using BAT R-package (Cardoso et al., 2022; Mammola and Cardoso, 2020). In addition, we computed for beetles the standardized effect size of the functional mean pairwise distances (ses mpd) and functional mean nearest taxon distances (ses mntd) based on the five quantitative traits and using the picante R-package (Kembel et al., 2020).

Finally, to calculate the cascading effects of forest dieback on environmental conditions and saproxylic beetles, we employed piecewise SEMs, using the piecewiseSEM R-package (Lefcheck et al., 2020). The models implemented in the SEM were linear regressions for which we log-transformed the variables that required it, in order to respect the linearity assumption. We also added a random variable using site (e.g. Aure and Sault in fir context). The SEM allow the construction of complex networks of relationships at multiple hierarchical levels (Lefcheck, 2016). In our SEMs, hierarchy was based on the direct effects of forest dieback on trees (i.e. woody elements) and consequently on TreMs, which both had subsequent effects on saproxylic beetles. Since we only tested the effect of forest dieback (i.e. only one tested effect) on woody element, we used the 5% α -error p.value to determine the significant effects. In contrast for TreMs, we tested both forest dieback and woody element metrics (i.e. 19 tested effects). Likewise for biodiversity, we tested both forest dieback and all environmental condition metrics (i.e. 31 tested effects). Therefore, we respectively adjusted the α -error p.value to 0.0026 (as the result of $\frac{0.05}{19}$) and 0.0016 (as the result of $\frac{0.05}{31}$).

Multivariate analysis

To estimate the differences in taxonomic and functional compositions along the forest dieback gradient, we computed taxonomic and functional dissimilarity (the β -diversity) between plots, based on beetle species abundance and using the "beta" and "kernel.beta" functions of the BAT R-package with Jaccard family (Cardoso et al., 2022; Mammola and Cardoso, 2020). For the functional compositions, we used the dissimilarity values between functional hypervolumes of each study plot. We employed PERMANOVA analysis to identify the consequences of forest dieback on taxonomic and functional compositions, using the vegan R-package (Oksanen et al., 2022; Tab. 6.1). For fir and oak forests we used the standardized forest dieback index, while for spruce forests we used the categorical index. In addition, through Canonical Analysis of Principal coordinates (CAP), we selected the environmental variables (Figs. 6.3 and 6.4) which significantly affected the inertia of taxonomic and functional compositions based on 999-run permutation tests (function "capscale" of the vegan R-package; Oksanen et al., 2022). We also added forest dieback (the quantitative index in fir and oak forests and the categorical index in spruce forests), and site (e.g. Aure and Sault in fir forests) to compare their effects with environmental metrics. We selected the significant metrics from all metrics by an iterative selection process based on the removal of

the metrics co-explaining the least inertia. As a result, the selected significant variables all co-explain the total inertia of the compositions (Tab. 6.2).

We also analysed the β -diversity of within-class dieback for both taxonomic and functional compositions. For this, we used the β -diversity matrices from the "beta" and "kernel.beta" functions from BAT R-package (Cardoso et al., 2022). In addition, we decomposed the within-class β -diversity values into their replacement and richness (i.e. gain/loss) components (Carvalho and Cardoso, 2020; Mammola and Cardoso, 2020).

6.3 Results

6.3.1 Response of taxonomic and functional α -diversity to environmental filtering and forest dieback

Overall, forest dieback led to a sharp increase in the dead wood amount together with a decrease in the living tree biomass (with the exception of oak forests; Figs. 6.5, 6.6, 6.7). In both fir and oak forests, this increase in quantity was followed by an increase in deadwood diversity (Figs. 6.5 and 6.6). In parallel, in spruce forests, forest dieback induced a lower level of deadwood trait richness (Fig. 6.6). Furthermore, in both fir and spruce forests, forest dieback induced an increase in the amounts of lying and standing deadwood, with a greater magnitude for lying deadwood in fir forests and for standing deadwood in spruce forests (Figs. 6.5 and 6.6). Forest dieback severity generally caused a decrease of substrate level (i.e. "CWM Substrate") followed by an increase of the trait dispersion (i.e. "FDis Substrate"; Figs. 6.5, 6.6, 6.7). In both fir and spruce forests, dieback also promoted the amount of highly decayed deadwood (Figs. 6.5 and 6.6). In addition, it induced an increase in the mean stage of decay value of woody elements in all study contexts (Figs. 6.5, 6.6, 6.7). Moreover, the dispersion of the stage of decay increase in fir and spruce forests, but not in oak forests (Figs. 6.5, 6.6, 6.7). Forest dieback caused an increase of the amount of both medium, and large & very large deadwood in the fir and spruce forests, with higher magnitude for large & very large deadwood in spruce forests, but not in oak forests (Figs. 6.5, 6.6, 6.7). However, the dispersion of deadwood diameter trait is increased by forest dieback in oak forests (Fig. 6.7).

In addition, forest dieback also caused changes in the composition of tree-related microhabitats (TreMs; Figs. 6.5, 6.6, 6.7). Also in fir forests, it increased the mean of TreM-bearing substrate types (i.e. TreMs are rather carried by living trees) and its heterogeneity (Fig. 6.5). Dieback in fir forests also increase the mean position height of TreMs in trees (Fig. 6.5). In addition, forest dieback decreased the mean ontogeny of TreMs (i.e. TreMs develop faster in disturbed stands), but increased the heterogeneity of ontogeny (Fig. 6.5). Furthermore, it induced a higher quantity of saproxylic TreMs (i.e. which contains deadwood tissues; Fig. 6.5). In spruce forests, forest dieback led to a decrease in the trait richness of TreMs, as has the trait richness of deadwood (Fig. 6.6). In parallel, in contrast to fir forests, dieback in spruce forests led to a decrease in the TreM-bearing substrate types (i.e. TreMs are rather borne by deadwood pieces; Fig. 6.6), but it increased the heterogeneity of the TreM-bearing substrate types (Fig. 6.6). Furthermore, in spruce forests, dieback did not change the vertical position of TreMs on the trees but induced a decrease in their position heterogeneity (Fig. 6.6). In addition, it increased both the mean wetness of the borne TreMs and the heterogeneity of wetness conditions (Fig. 6.6). Forest dieback also led to a decrease in the mean life span of TreMs, but in parallel to an increase in their life span heterogeneity (Fig. 6.6). To conclude with spruce forests, forests dieback, as in fir forests, increased the mean amount of saproxylic TreMs (Fig. 6.6). In contrast, in oak forests, we did not observed any effects of forest dieback on TreM composition (Fig. 6.7).

These effects of forest dieback on resource and habitat conditions did partially affect variables of taxonomic and functional α -diversity in fir and spruce forests, but not in oak forests (Figs. 6.5, 6.6, 6.7). In fir forests, weighted means of both TreM wetness and saproxylic did positively affect saproxylic beetle

species richness (Fig. 6.5). In spruce forests, the amount of large and very large deadwood pieces did positively affect saproxylic beetle functional divergence (Fig. 6.6). In addition, mean TreM life span had negative effect on beetle species richness (Fig. 6.6). Finally, in spruce forests, the beetle functional evenness was negatively affected by TreM diversity but was also positively affected by the heterogeneity of TreM-bearing substrate types (Fig. 6.6).

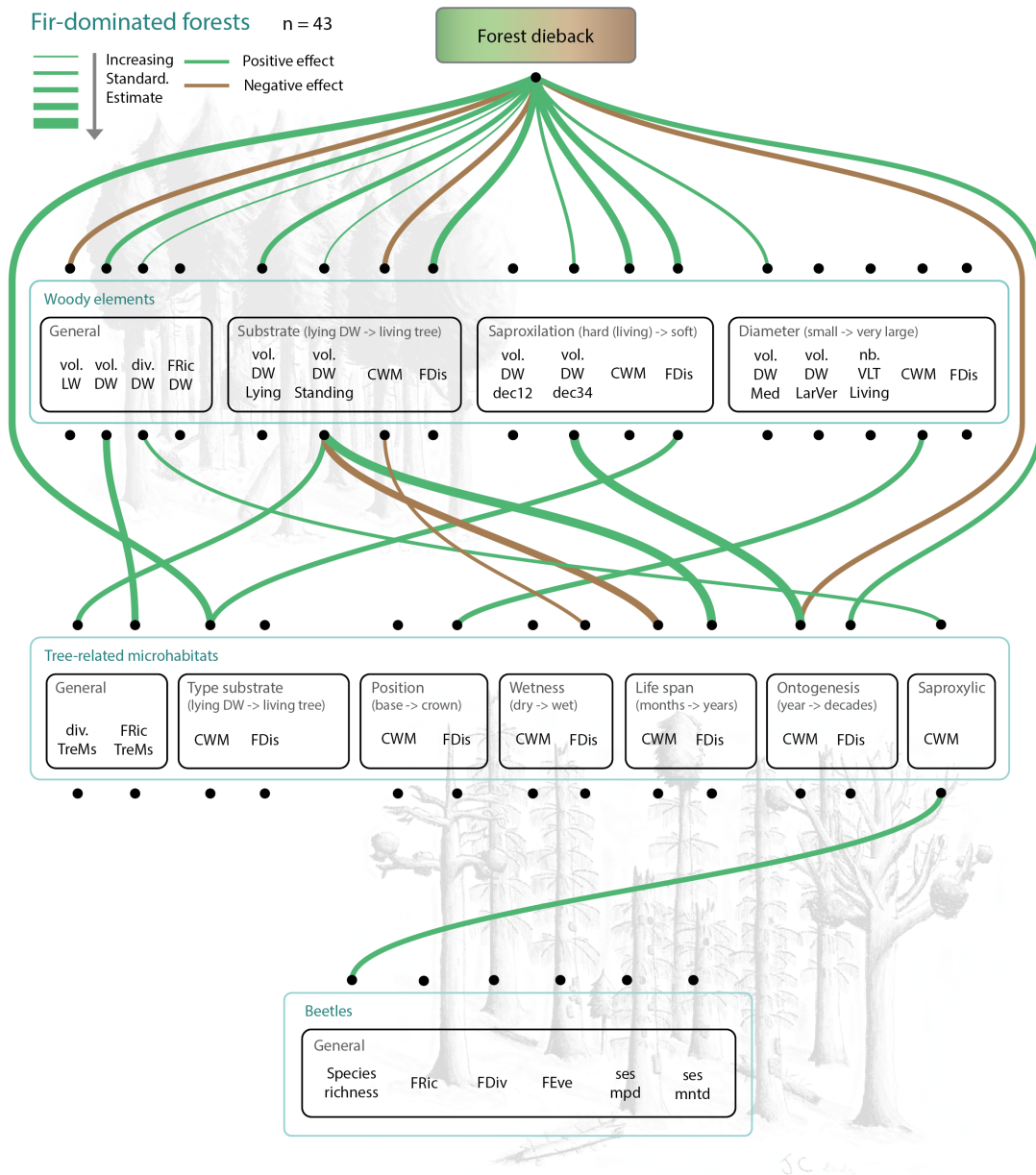


Figure 6.5 – Results from structural equation modelling (SEM) for fir-dominated forests (Pyrenees region, drought disturbance). The structure of SEM is "forest dieback -> woody elements -> tree-related microhabitats -> saproxylic beetles". Woody element variables being tested for only one effect (effect of forest dieback), significant effects are shown at $p < 0.05$. In contrast, TreMs and saproxylic beetle variables being tested respectively for 19 and 31 potential effects, significant effects are shown at $p < 0.0026$ and $p < 0.0016$. Green lines show positive effects and brown lines negative ones. Line widths illustrate the magnitude of effects (standardized estimates).

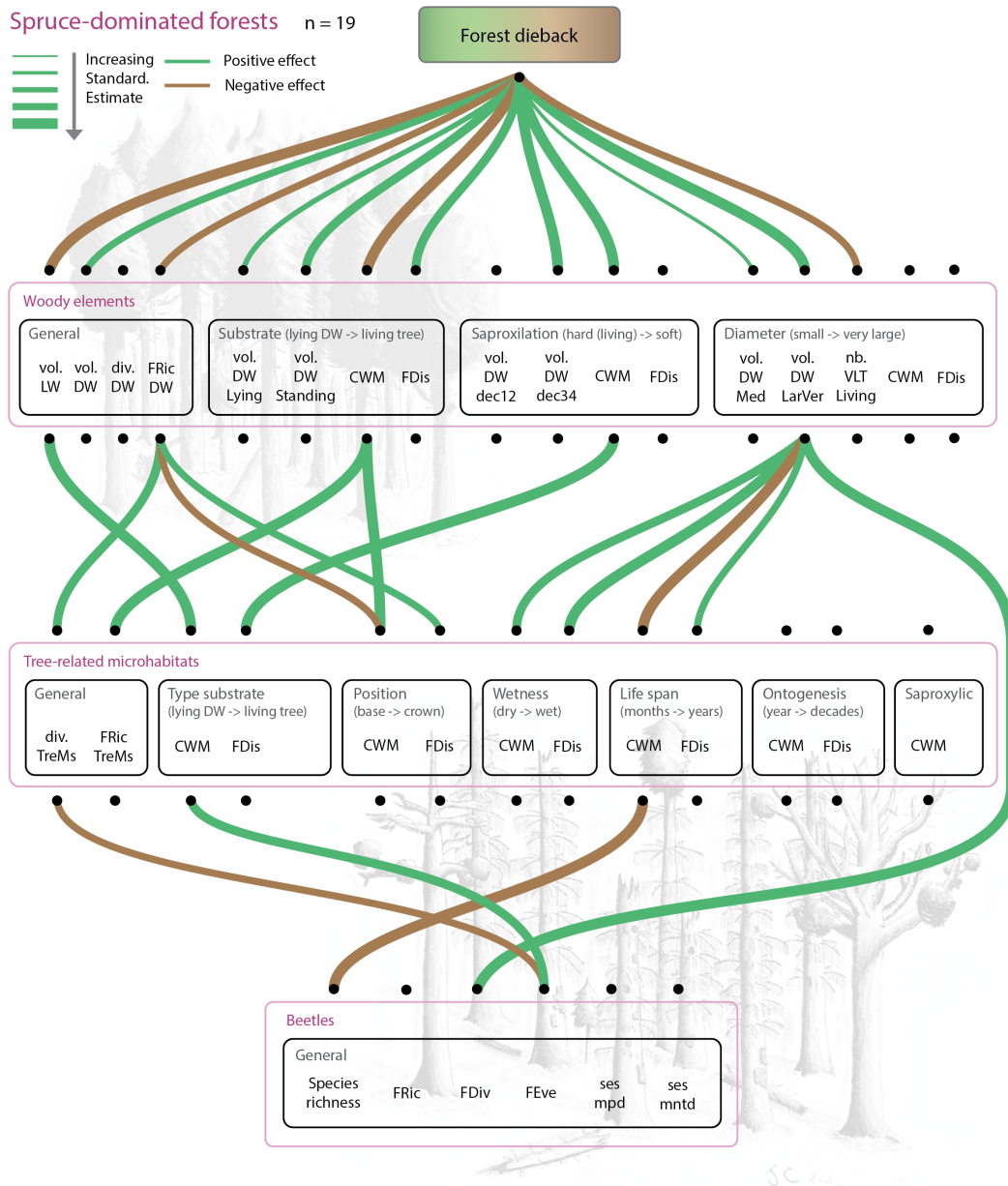


Figure 6.6 – Results from structural equation modelling (SEM) for spruce-dominated forests (Bavaria region, bark beetle disturbance). The structure of SEM is "forest dieback -> woody elements -> tree-related microhabitats -> saproxylic beetles". Woody element variables being tested for only one effect (effect of forest dieback), significant effects are shown at $p < 0.05$. In contrast, TreMs and saproxylic beetle variables being tested respectively for 19 and 31 potential effects, significant effects are shown at $p < 0.0026$ and $p < 0.0016$. Green lines show positive effects and brown lines negative ones. Line widths illustrate the magnitude of effects (standardized estimates).

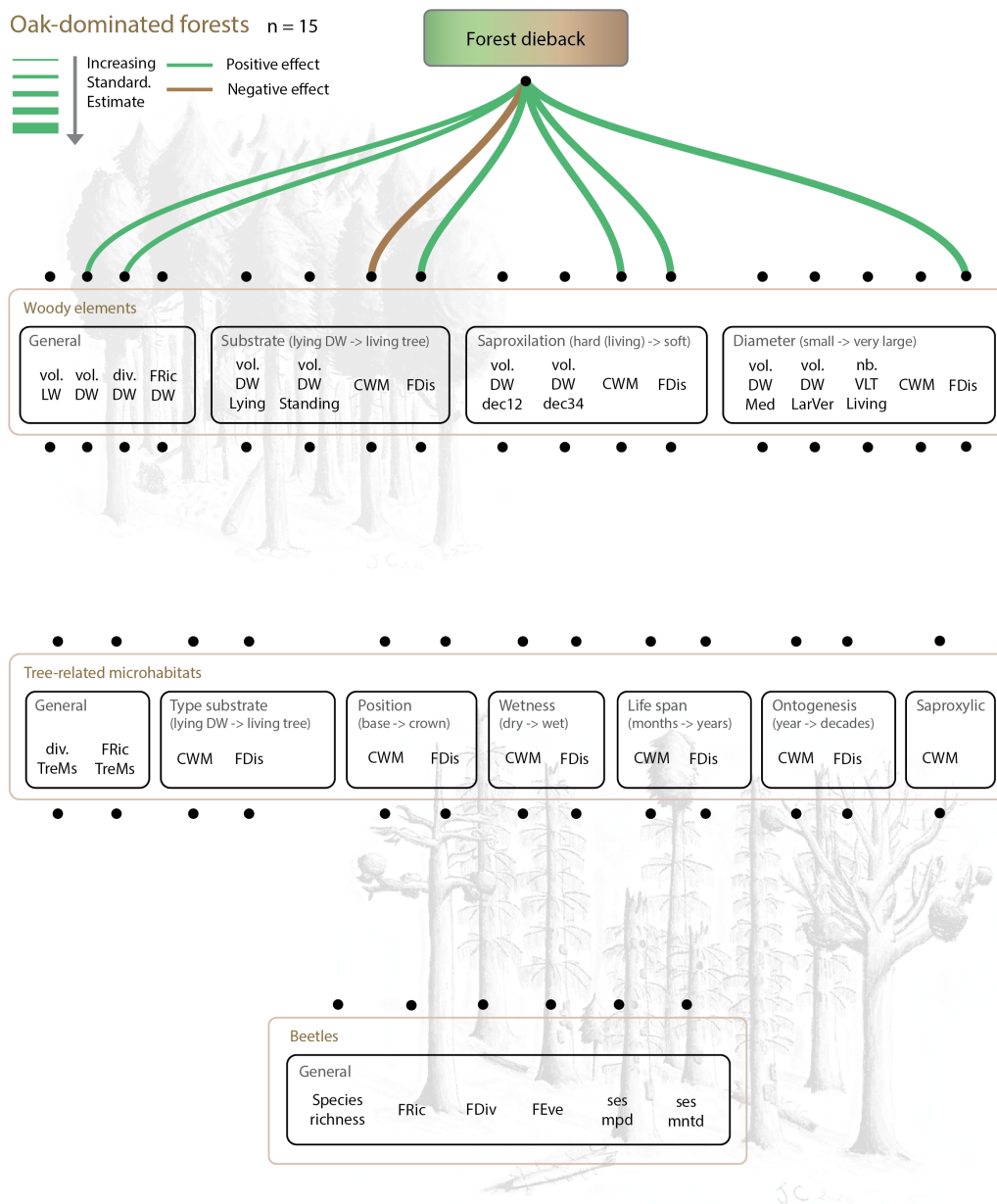


Figure 6.7 – Results from structural equation modelling (SEM) for oak-dominated forests (Loire region, drought disturbance). The structure of SEM is "forest dieback -> woody elements -> tree-related microhabitats -> saproxylic beetles". Woody element variables being tested for only one effect (effect of forest dieback), significant effects are shown at $p < 0.05$. In contrast, TreMs and saproxylic beetle variables being test respectively for 19 and 31 potential effects, significant effects are shown at $p < 0.0026$ and $p < 0.0016$. Green lines show positive effects and brown lines negative ones. Line widths illustrate the magnitude of effects (standardized estimates).

6.3.2 Responses of taxonomic and functional compositions of saproxylic beetles to environmental filtering and forest dieback

Fir-dominated forests

We did not observe any differences in taxonomic and functional compositions in response to forest dieback (Tab. 6.1). In contrast, we showed significant responses of taxonomic composition to the site variable, but also to the dead wood diversity and trait richness (Tab. 6.2). Nonetheless, functional composition did not respond to any environmental metrics (Tab. 6.2).

Furthermore, on the one hand, we did not observe significant difference of the within-class taxonomic β -diversity in response to forest dieback (Fig. 6.8). On the other hand, we showed a significant decrease in the within-class functional β -diversity between *Low* and *Mid* forest dieback ($p < 0.01$; Fig. 6.8). However, there were no other differences between *Low* and *High* forest dieback (Fig. 6.8). Regarding after partitioning the within-class β -diversity for taxonomic and functional compositions, we noticed significant differences of their components in response to forest dieback (Fig. 6.9). There was a significant increase in replacement and a decrease in the richness components of taxonomic β -diversity between *Low* and *Mid* forest dieback (Fig. 6.9). Similarly, we observed a significant increase in replacement and a decrease in richness across the forest dieback gradient for functional β -diversity (Fig. 6.9).

Table 6.1 – Results from PERMANOVA analysis on taxonomic and functional compositions in response to forest dieback (the numerical gradient in fir and oak forests and categorical in spruce forests). The analysis were stratified by site (e.g. Aure and Sault in fir forests).

Composition	R ²	p.value
Fir-dominated forests		
Taxonomic	0.061	0.172 ^{ns}
Functional	0.009	0.976 ^{ns}
Spruce-dominated forests		
Taxonomic	0.123	0.002**
Functional	0.09	0.268 ^{ns}
Oak-dominated forests		
Taxonomic	0.143	0.062 ^{ns}
Functional	0.125	0.054 ^{ns}

Table 6.2 – Environmental drivers of variation in saproxylic beetle compositions (both taxonomic and functional). Results are from the Canonical Analysis of Principal coordinates analysis.

Taxonomic composition			Functional composition		
Environmental variables	F.value	R ²	Environmental variables	F.value	R ²
Fir-dominated forests					
Site	7.5***				
div. DW	2.9***	0.24	No significant var.		
FRic DW	2.2**				
Spruce-dominated forests					
TreMs FDis Position	1.7**	0.16	DW FDis Type substrate	2.6**	0.23
TreMs CWM Position	1.6**		TreMs FDis Type substrate	2.2**	
Oak-dominated forests					
TreMs CWM Life span	2.2**	0.14	TreMs CWM Position	3.9**	0.38
			TreMs CWM Life span	3.4**	

DW = "dead wood"; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Spruce-dominated forests

In contrast with fir forests, we observed a taxonomic composition change in spruce forests due to the forest dieback ($p < 0.01$), but not for the functional composition (Tab. 6.1). In addition, the taxonomic composition appeared to be significantly affected by the mean and heterogeneity of TreM vertical position on trees (Tab. 6.2). In parallel, the functional composition was affected by the heterogeneity of woody substrate (Tab. 6.2).

Furthermore, we did not show differences in within-class β -diversity in response to forest dieback, neither for taxonomic nor for functional compositions (Fig. 6.8). In contrast, we observed a significant increase in replacement ($p < 0.001$) and a decrease in richness ($p < 0.01$) components due to forest dieback for the taxonomic β -diversity (Fig. 6.8). In addition, we showed a significant increase in functional replacement due to forest dieback but no difference in the richness component (Fig. 6.8).

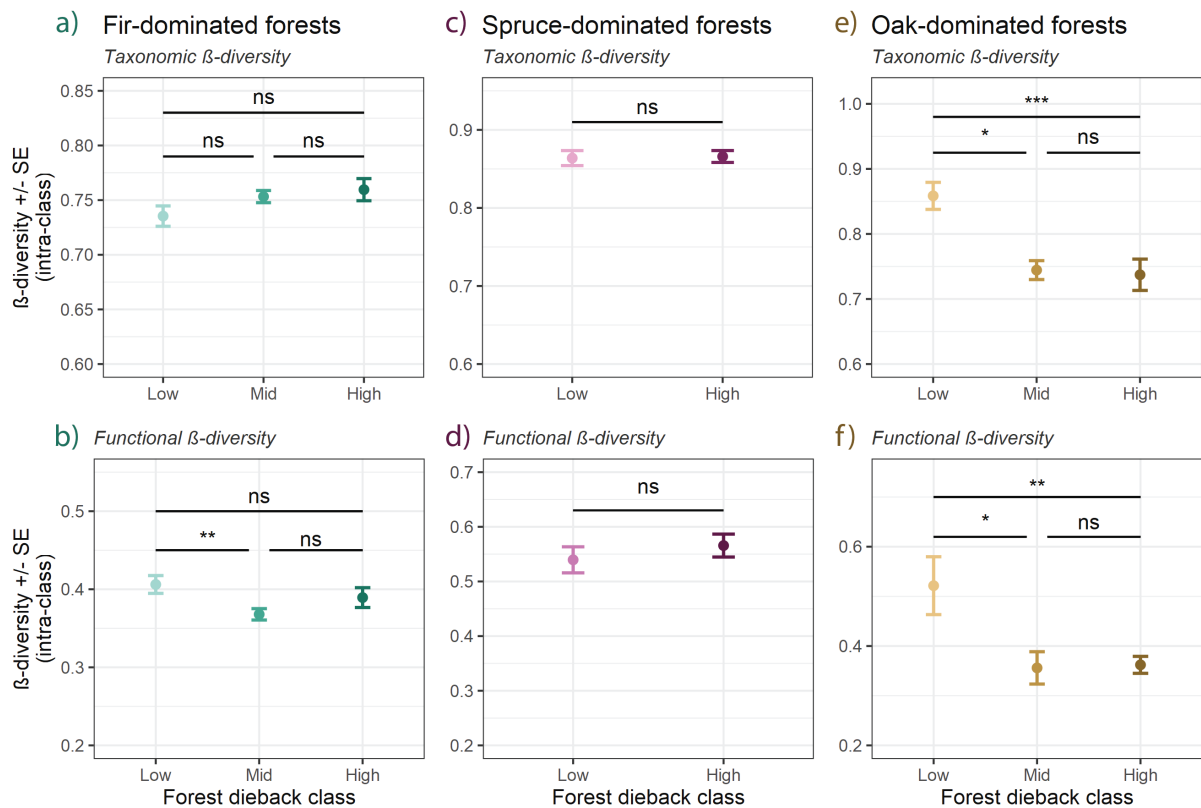


Figure 6.8 – Taxonomic (top) and functional (bottom) β -diversity mean (intra-class values) for low-, mid- and high-dieback forests in each study context (left: fir, middle: spruce, right: oak forests). Tests of comparisons were done using ANOVA tests. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Oak-dominated forests

As in fir forests, we did not observe differences in taxonomic and functional compositions in response to forest dieback in oak forests (Tab. 6.1). Furthermore, we showed that taxonomic composition was significantly affected by the mean life span of TreMs while functional composition was mainly affected by mean vertical position and also life span of TreMs (Tab. 6.2).

In addition, with regard to within-class β -diversity, we noted significant decreases for both taxonomic and functional compositions due to forest dieback (Fig. 6.8). Moreover, for both taxonomic and functional composition, the decrease is much more significant between *Low* and *High* dieback (i.e. respectively p

< 0.001 and $p < 0.01$) than between *Low* and *Mid* dieback classes (i.e. $p < 0.05$; Fig. 6.8). However, regarding the partitioning of within-class β -diversity, we did not notice significant change due to forest dieback for taxonomic composition (Fig. 6.9). Regarding the functional composition, we also did not observe difference in replacement component, but we did observe a significant decrease in richness between *Low* and *High* forest dieback (Fig. 6.9).

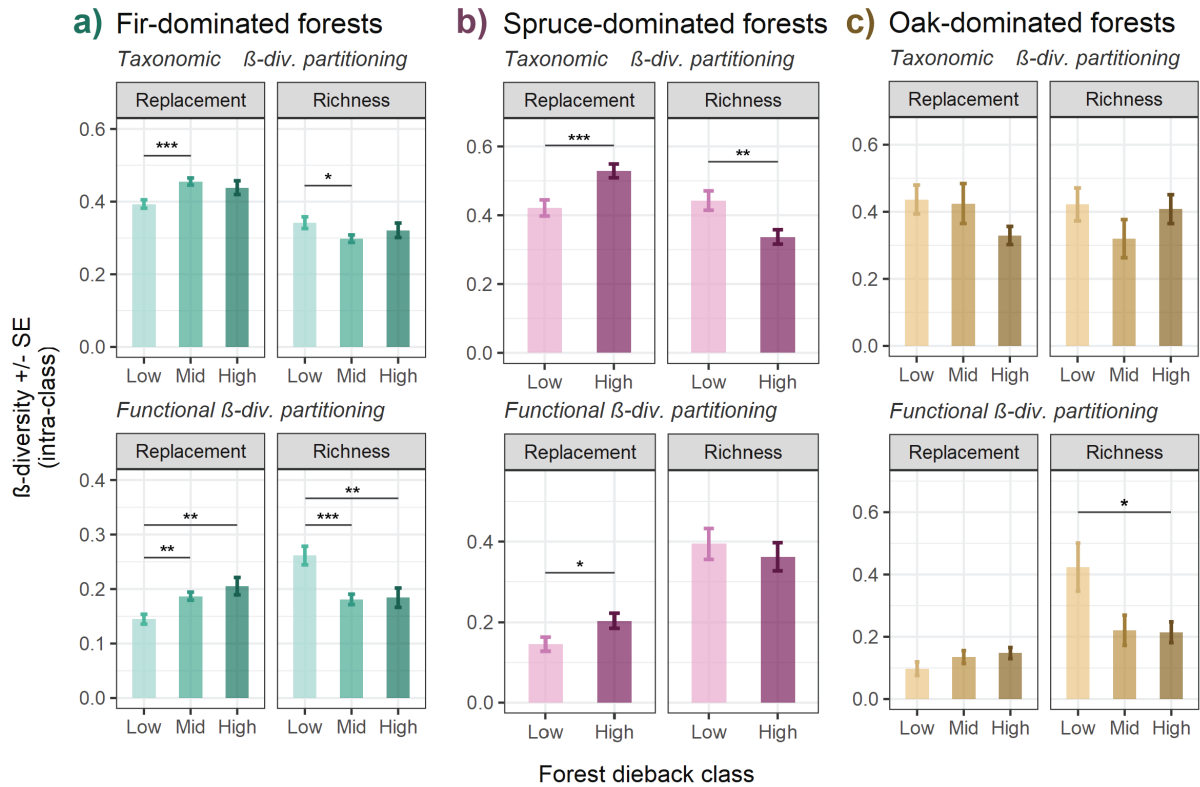


Figure 6.9 – Taxonomic (top) and functional (bottom) β -diversity partitioning according to study context (a: fir, b: spruce, c: oak forests) and forest dieback. Tests of comparisons were done using ANOVA tests and post-hoc Tukey tests. In spruce forest, since there is only two classes, Student's test was applied. ns = $p \geq 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

6.4 Discussion

6.4.1 Saproxylic beetles responded to changes in abiotic conditions due to natural disturbances

α -diversity response

Natural disturbances in all three contexts led to tremendous transformations in forest resources with strong effects on trees and their borne TreMs (Figs. 6.5, 6.6 and 6.7). These transformations induced cascading modifications on saproxylic beetles taxonomic and functional composition. Firstly, in fir forests, the increase mean value of saproxylic TreMs generated by drought disturbances induced an increase in richness of saproxylic beetle species (Fig. 6.5). This effect would be supported by habitat-heterogeneity hypothesis since higher mean value of saproxylic trait displayed both higher amount and diversity of saproxylic TreMs as many more niches available for saproxylic beetles (Seibold et al., 2016). Surprisingly, we did not noticed any effects of dead wood on beetle α -diversity.

In parallel, in spruce forests, the increased heterogeneity of TreM-bearing substrate types, a proxy of resource heterogeneity, led to an increase of the functional evenness (Fig. 6.6). Consequently, the increasingly heterogeneity of TreM-bearing substrate types and, therefore, the increasing amount of new potential niches, led to a greater regularity of trait values in the functional spaces (Mouillot et al., 2013). This greater regularity of trait values would be the result of a lesser environmental filtering resulting from a greater niche diversification due to disturbances and allow an effective occupation of the range of available resources in spruce forests (Mason et al., 2005; Sitters et al., 2016). Furthermore, also in spruce forests, disturbances led to a significant increase in the amount of large and very large dead wood, which had a positive effect on the functional divergence of saproxylic beetles (Fig. 6.6). As a result, beetle abundances are distributed towards the extremes values of functional space in response to dieback, which could be a consequence of less competition for resources and greater efficiency in resource use (Mason et al., 2005). Finally, in spruce forests, species richness has benefited from forest dieback due to the reduced average life span of TreMs (Fig. 6.6). Compounded windstorm and bark beetle outbreaks in spruce forest led to rapid shifts in tree conditions bearing new less durable TreMs (e.g., annual polypores). These rapid changes would have created valuable new niches for saproxylic beetles, thus increasing species richness.

Finally, in oak forests, we surprisingly observed no response of saproxylic beetle α -diversity to changing environmental conditions due to forest dieback (despite significant changes in dead wood resources; Fig. 6.7). This absence of effect in oak forests would be the result of several reasons. The salvage logging of the most valuable trees led to a lower dead wood amount and diversity in oak forests than in the two other study context. Müller and Bütler (2010) showed that the response of saproxylic organisms to the dead wood amount is non-linear with e.g., threshold at 30-50 m³/ha of dead wood for lowland oak-beech forests. The global average amount of 21 m³/ha and of 42 m³/ha in high class of dieback would be insufficient to support higher α -diversity of saproxylic beetles. In addition, also in oak forests, we did not notice any changes in the composition of TreMs due to forest dieback while they appear of great interest for beetle α -diversity in the two other contexts. This non-response could be the result of both salvage logging and of the slower decomposition process of oak dead wood due to higher physical and chemical barriers than in fir and spruce species (Ulyshen, 2016). This slower decomposition would end by a lower rate of appearance of new TreMs that would normally represent new niches for saproxylic beetles.

Response of between-class β -diversity

In fir forests, neither taxonomic nor functional compositions responded to forest dieback (Tab. 6.1). The taxonomic non-response was not a surprise since it has been already shown in former studies (Cours et al., 2021; Sire et al., 2022). Similarly, the functional non-response is not a surprise either, as we have previously shown that each quantitative functional traits did not respond to local but to landscape dieback (Cours et al., 2021, 2022). It seems that the amount of dead wood generated by the drought disturbance was not sufficient to support new saproxylic beetle compositions, both taxonomically and functionally. Nonetheless, we observed significant responses of beetle taxonomic composition to the diversity and the trait richness of dead wood while dead wood diversity was also positively affected by forest dieback (Tab. 6.2, Fig. 6.5). The diversity and the trait richness of dead wood are both proxies of the diversity of available dead wood niches for saproxylic beetles. Consequently, saproxylic beetles taxonomic composition seemed to be significantly affected by the amount of available niches. By contrast, the functional composition unexpectedly did not respond to the environmental gradients studied. This could be the result of the absence of particular environmental gradients in our sampling design, such as canopy openness, which appears to be very important for saproxylic beetles and is generally strongly affected by disturbances (Bouget et al., 2014a; Edelmann et al., 2022; Lettenmaier et al., 2022; Seibold et al., 2016).

Furthermore, in spruce forests, the taxonomic composition responded significantly to forest dieback (p

< 0.01), but not the functional composition (Tab. 6.1). The significant response in taxonomic composition is consistent with previous results (Cours et al., 2021; Georgiev et al., 2022). By contrast, the absence of response in functional composition was a surprise since we previously showed that spruce dieback did affect average community values of functional traits (Cours et al., 2021). As a result, there was no shift in the position of functional spaces along the range of trait value in response to forest dieback. The parallel increase in functional divergence and evenness indirectly due to dieback indicates that there were only changes in the distribution of traits within the functional spaces. Furthermore, the separate taxonomic and functional response showed that while species have changed, the theoretical niches of the community have not. Nonetheless, both taxonomic and functional compositions responded to different environmental gradients (Tab. 6.1). Taxonomic composition was affected by the TreM vertical position in trees and the heterogeneity of this position. We saw that the compound windstorm and bark beetle outbreak had negatively affect the heterogeneity of TreM vertical position in trees, and thus could had indirectly influence the beetle taxonomic composition. In parallel, functional composition mainly responded to the heterogeneity of both substrate type and TreM-bearing substrate type. This result is in accordance with the previous positive effect of the heterogeneity of TreM-bearing substrate type on functional evenness. The response of the functional composition to substrate type heterogeneity would be another indication of a greater diversity of available niche due to forest dieback and leading to less competition for and better use of resources by saproxylic beetles (Mason et al., 2005).

Finally, in oak forests, neither taxonomic nor functional compositions responded to forest dieback (Tab. 6.1). In parallel, they both respond to TreM trait gradients (Tab. 6.1). The taxonomic composition was affected by the mean TreM life span and the functional composition by the additional effects of average TreM vertical position and life span. Consequently, since disturbances had no effects on TreM composition in oak forests, it would not have any indirect effect on beetle compositions.

The overall absence of response of functional composition to forest dieback would indicate a major process of resource supplementation for saproxylic beetles (Dunning et al., 1992; Taylor et al., 1993). Indeed, in the case of complementation process, forest dieback would create new resources colonised by new species with new traits and thus, would change in cascade the functional space. In the absence of such changes, forest dieback must have resulted in a supplementation of already existing resources in the landscape. In parallel, the observed changes in taxonomic and functional α -diversity components indicate that natural disturbances should allow the local concentration of these existing but scattered resources across the landscape. However, these effects of natural disturbances appear to be non-linear and depend strongly to the disturbance severity and/or spatial extent (Cours et al., 2021, 2022; Kortmann et al., 2022; Müller and Bütler, 2010). For instance, Kortmann et al. (2022) showed that colonisation of disturbed areas by new beetle species occurs at a high level of disturbance severity (76%-97%).

6.4.2 Forest dieback has led to the homogenisation and/or generalisation of saproxylic beetle assemblages in the landscape

In fir forests, forest dieback did not significantly affect taxonomic within-class β -diversity but induced a significant decrease between *Low* and *Mid* classes ($p < 0.01$; Fig. 6.8). In contrast, the β -diversity partitioning displayed many results. The increase in the replacement component and the decrease in the richness component, both for taxonomic and functional β -diversity, would demonstrate greater community stability following forest dieback. Indeed, the increase in the replacement component and/or the decrease in the richness component is the result of a greater species turnover between plots of the same class (the replacement of one species or trait by another) and a lower fluctuation in richness (gain/loss). This greater stability appears even higher for the functional composition (Fig. 6.9).

Spruce forests followed a similar pattern as in fir forests: the overall β -diversities were not affected by forest dieback while β -partition displayed changes in within-class β -diversity (Figs. 6.8 and 6.9). Similarly, the replacement component increased and the richness component decreased due to forest

dieback. In contrast, changes in spruce forests were more important for the taxonomic composition than for the functional composition. This would indicate a greater species stability in the *High* dieback class plots than in the *Low* dieback class.

By contrast, in oak forests, we observed a large decrease of the overall β -diversity of saproxylic beetles due to forest dieback, indicating an homogenization of both taxonomic and functional compositions among plots (Fig. 6.8). Georgiev et al. (2022) observed very similar pattern of response in German spruce forests disturbed by windstorm. In parallel, we showed few changes in the within-class β -diversities with only a significant reduction of richness component of functional component between *Low* and *High* dieback classes ($p < 0.05$).

The process of community stabilisation and/or homogenisation observed in response to forest dieback would additionally indicate, with the absence of response of functional compositions, a process of resource supplementation across landscape due to forest dieback. Dead wood and some TreMs that exist in managed and intact forests but are scattered across the landscape, have increased in quantity everywhere due to natural disturbances (i.e. supplementation of an existing but rare resource). Subsequently, this resource generalisation at landscape scale would end by local beetle species saturation due to the form of the species-area relationship, leading to the stabilisation and/or homogenisation of the community across the landscape. This hypothesis is further strengthened by the indirect positive effect of forest dieback on local α -diversity in both fir and spruce forests. However, these consequences of forest dieback on saproxylic beetle assemblages appears to be non-linear and are mediated by thresholds in resource quantities. Furthermore, supplementation seems to be the main mechanism explaining the observed community stabilisation and/or homogenisation but complementation have been also observed for some very rare beetle species requiring very particular resource (e.g., *Peltis grossa* L. species in Bavaria forests; Busse et al., 2022).

6.5 Supplementary material

Supplementary materials for this chapter can be found in appendix D.

Part IV

Consequences of local and landscape forest dieback on biodiversity

Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales

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Abstract

Context Many forest ecosystems around the world are facing increasing drought-induced dieback, causing mortality patches across the landscape at multiple scales. This increases the supply of biological legacies and differentially affects forest insect communities.

Objectives We analysed the relative effects of local- and landscape-level dieback on local saproxylic beetle assemblages. We assessed how classical concepts in spatial ecology (e.g., habitat-amount and habitat-patch hypotheses) are involved in relationships between multi-scale spatial patterns of available resources and local communities.

Methods We sampled saproxylic beetle assemblages in commercial fir forests in the French highlands. Through automatic aerial mapping, we used percentage of dead tree crown pixels to assess dieback levels at several nested spatial scales. We analysed beetle taxonomic, phylogenetic and functional diversity related to differing levels of multi-scale dieback.

Results We found that taxonomic, functional, and phylogenetic diversity of saproxylic beetle assemblages significantly benefitted from forest dieback, at both local and landscape scales. We detected significant effects in the multiplicative models combining local and landscape variables only for phylogenetic diversity. Increased landscape-scale dieback also caused a functional specialisation of beetle assemblages, favouring those related to large and well-decayed deadwood.

Conclusions Increasing tree mortality under benign neglect provides conservation benefits by heterogenising the forest landscape and enhancing deadwood habitats. Legacy retention practices could take advantage of unharvested, declining forest stands to promote species richness and functional diversity within conventionally managed forest landscapes.

Keywords: Scale of effect; Saproxylic beetles; Climate change; Forest decline; Drought; Disturbance legacy

Résumé

Contexte Beaucoup d'écosystèmes forestiers à travers le monde font de plus en plus face à des dépérissements causés par des sécheresses. Ces derniers augmentent l'apport d'héritage biologiques et affectent différemment les communautés d'insectes forestiers.

Objectifs Nous analysons les effets relatifs des niveaux de dépérissement aux échelles locale et paysagère sur les assemblages locaux de coléoptères saproxyliques. Nous avons évalué de quelle manière les concepts classiques d'écologie du spatial (e.g., les hypothèses de quantité d'habitat et de patch d'habitat) sont impliqués dans les relations entre les configurations spatiales multi-échelles des ressources disponibles et les communautés locales.

Méthode Nous avons échantillonné les assemblages de coléoptères dans les forêts de sapin de montagne sous gestions. À travers une cartographie aérienne automatique, nous avons utilisé le pourcentage de pixels de couronnes d'arbre mortes en tant qu'évaluation du niveau de dépérissement à différentes échelles spatiales emboîtées. Nous avons alors analysé la réponse des diversités taxonomique, fonctionnelle et phylogénétique aux différents niveaux de dépérissement multi-échelles.

Résultats Nous avons mis en avant que les diversités taxonomique, fonctionnelle et phylogénétique des assemblages de coléoptères saproxyliques ont significativement bénéficié du dépérissement forestier, tant à une échelle locale que paysagère. Nous n'avons détecté des effets significatifs dans les modèles multiplicatifs combinant des variables locale et paysagère, que pour la diversité phylogénétique. Une augmentation du dépérissement à l'échelle du paysage a aussi causé une spécialisation fonctionnelle des assemblages de coléoptère, favorisant ceux associés à de gros bois morts fortement décomposés.

Conclusions L'augmentation de la mortalité des arbres associé à une stratégie de rétention des héritages fournit des bénéfices de conservation à travers l'hétérogénéisation du paysage forestier et l'amélioration des habitats bois mort. Les pratiques de conservation des héritages pourraient tirer parti des peuplements forestiers non exploités et dépérissants pour promouvoir la richesse des espèces et la diversité fonctionnelle dans les paysages forestiers gérés de manière conventionnelle.

Mots-clés: Echelle de l'effet; Coléoptères saproxyliques; Changement climatique; Dépérissement forestier; Sécheresse; Héritage de perturbation

7.1 Introduction

Natural disturbances are major drivers of forest spatial and temporal dynamics (Bowd et al., 2021b; Kuuluvainen, 2016; Pickett and White, 1985). Multiple disturbance complexes shape the structural heterogeneity of forests and generate key resources such as tree-related microhabitats, canopy gaps, snags, and logs, generally referred to as disturbance legacies (Franklin et al., 2000; Johnstone et al., 2016), which are colonised by diverse, and often specific communities (Kuuluvainen, 2016; Lachat et al., 2016; Swanson et al., 2011). Among them, saproxylic beetles are a highly diverse group of insects that depend on dead or decaying wood for at least part of their life cycle and play important ecological roles by participating in carbon and nutrient cycles or by complexifying trophic chains (Stokland et al., 2012). However, current silvicultural practices tend to reduce deadwood-related resources and microhabitats (Courbaud et al., 2022; Grove, 2002; Paletto et al., 2014; Siitonen, 2001). As a consequence, saproxylic beetles are at considerable risk in intensively managed forests (Grove, 2002; Seibold et al., 2015), and 17.9% of saproxylic beetle species are now considered threatened in Europe (Calix et al., 2018).

Climate change alters natural disturbance regimes: warmer and drier conditions facilitate drought, wildfire, and insect outbreaks (Seidl et al., 2017). Lately, several large drought-related dieback events

have been reported (Sangüesa-Barreda et al., 2015), and a further increase in drought-induced dieback and decline in terms of frequency, intensity, and spatial extent is expected to arise (Allen et al., 2010; Samaniego et al., 2018). As a consequence, deadwood supply, number of tree-related microhabitats and canopy openness are likely to increase and this may favour saproxylic populations (Cours et al., 2021; Müller et al., 2010; Sallé et al., 2020, 2021; Thorn et al., 2017); see chapter 5. Several local-scale (i.e. less than 0.5 ha) studies have highlighted different positive relationships between saproxylic beetle populations and forest dieback: (i) pest-related dieback from large outbreaks of spruce bark beetles (*Ips typographus*, Linnaeus, 1758) resulted in an increase in saproxylic beetle species richness, including many red-listed species (Beudert et al., 2015; Cours et al., 2021) and (ii) drought-related dieback of *Quercus* spp. also increased saproxylic beetle species richness (Sallé et al., 2020). It has therefore been hypothesised that declining stands may improve habitat conditions for threatened forest communities such as saproxylic beetles (e.g., Kašák and Foit, 2018; Müller et al., 2010; Sallé et al., 2021). However, these studies have mainly focused on local conditions, regardless of the severity of forest dieback at broader scales. Yet, many previous studies have highlighted the fact that the diversity and structure of local saproxylic beetle communities may also depend on large scale, i.e. landscape, conditions (e.g., Franc et al., 2007; Gibb et al., 2006; Haeeler et al., 2021; Økland et al., 1996). Sampling area size influences the detection of biodiversity responses to environmental conditions, a phenomenon known as "the scale of effect" (Jackson and Fahrig, 2015; Levin, 1992; Wiens, 1989). Insects are often highly mobile; they spread across landscapes in search of new resources, habitats, and/or reproductive partners (Janssen et al., 2016; Komonen and Müller, 2018; Ranius, 2006) and this mobility may result in potentially large scales of effect (Bergman et al., 2012; Seibold et al., 2017).

The relationship between spatial patterns of available resources and the number of associated species has been explored through several concepts based on ecological mechanisms. Within a given sampling area, the "habitat-amount hypothesis" predicts that the cumulative amount of habitat patches at the landscape scale better explains species richness than does local patch size (Fahrig, 2013; Seibold et al., 2017). In contrast, the "habitat-patch hypothesis", based on island-biogeography theory, assumes that local species richness is mainly restricted by local patch size and isolation (Fahrig, 2013; MacArthur and Wilson, 1967; Seibold et al., 2017). The "resource concentration hypothesis" predicts that the occurrence of a particular resource patch in the landscape induces a concentration of the species specialising on that resource, while at the same time, over-availability of that particular resource, exceeding the reproductive and colonising capacity of the associated species, could lead to a "dilution effect" (i.e. a large amount of substrate could lead to a reduction in the species load colonising the substrate; Otway et al., 2005). Hence, assessing the relative contribution of both local and landscape conditions on local biodiversity may well be critical; unfortunately, it is often challenging (Ammer et al., 2018). In recent decades, remote sensing and aerial photography have been widely used to monitor forest conditions and forest disturbances such as fires, defoliation or deforestation at large and nested spatial scales (e.g., Lambert et al., 2013; Senf and Seidl, 2021a).

Furthermore, most studies focus on the taxonomical responses of biological communities to forest dieback (Cai et al., 2021, but see Kozák et al., 2021; Sire et al., 2022; Thorn et al., 2014). Nonetheless, phylogenetic and functional diversity are highly relevant indicators of ecosystem functioning (Devictor et al., 2010). Phylogenetic diversity reflects the evolutionary history of a community through lineage relatedness while functional diversity reflects the diversity of the phenotypical traits selected by a particular environment, i.e. biotic and abiotic filters (Devictor et al., 2010; Kozák et al., 2021). Consequently, few studies have monitored taxonomic, functional, and phylogenetic responses of arthropods to forest disturbances at various spatial scales (Kozák et al., 2021).

In our study, we investigated how multi-scale forest dieback shaped local saproxylic beetle assemblages through several diversity dimensions. We analysed aerial photographs with machine-learning algorithms to map dead tree crowns and monitor dieback in silver fir forests in the French Pyrenees. After assessing

dieback level at several nested spatial scales, we focused on the taxonomic (α -diversity), phylogenetic, and functional responses of local saproxylic beetle assemblages to the multi-scale spatial structure of the forest dieback. This analysis would be seen as a progress of results from Cours et al., (2021, see chapter 5) in which we only studied consequences of local forest dieback on local saproxylic beetle assemblages. Finally, through multiplicative models (with interaction), we investigated subsequent mechanisms of forest dieback effects on the saproxylic beetle assemblages.

As a consequence of the increase in deadwood amount and light availability, we expected positive responses from the saproxylic beetle assemblages along the gradient of forest dieback at several spatial scales (Bouget et al., 2014a; Müller et al., 2010; Seibold et al., 2016). We also expected positive responses from several substrate guilds: firstly wood-eating species, due to an increase in the amount of deadwood; secondly, fungicolous species, due to an increase in the abundance of saprolignivorous fungal fruiting bodies; and thirdly, cavicolous species, due to an increase in the number of cavities in dying trees (Cours et al., 2021; Ojeda et al., 2007; Sallé et al., 2021). In addition, we predicted community preferences for larger and more decayed deadwood along the dieback gradient, resulting from the increased amount of deadwood (Gossner et al., 2013). Furthermore, we expected an increase in functional and phylogenetic diversity of saproxylic beetles, mainly due to the increase in deadwood diversity (as a proxy of niche diversity; Cours et al., 2021; Seibold et al., 2016). In parallel, saproxylic beetles having relatively great dispersal capacities (Komonen and Müller, 2018; Ranius, 2006), we expected greater responses to landscape conditions, than local one (Seibold et al., 2017). Finally, we tested the interactive effects between the local and landscape scales on local saproxylic beetle assemblages, expecting no significant interactions since both scales should additionally affect assemblages (Seibold et al., 2017).

7.2 Materials and methods

7.2.1 Site description

A total of 56 plots were chosen in montane forests dominated by silver fir (*Abies alba* Mill.). The plots were located in two montane regions in the French Pyrenees: 28 plots in the Aure Valley in the Central Pyrenees (854 to 1570 m a.s.l., 1298 m on average; 42° 51'46.8" N 0° 36'08.9" E) and 28 plots on the limestone Sault Plateau in the Eastern Pyrenees (705 to 1557.3 m a.s.l., 1029 m on average; 42° 50'58.7" N 2° 00'41.3" E) (Fig. 7.1). The average distance between study plots was 860 m (standard deviation (SD) \pm 469 m), with a minimum value at 296 m and a maximum at 2439 m. Forests occupied 50% of the Aure Valley and 75% of the Sault region (Fig. 7.1). Silver fir dominated in 70% (95% confidence interval (CI95) \pm 12%) of the forests surrounding our plots in the Aure Valley and in 88% (CI95 \pm 5%) of the forests on the Sault Plateau. The secondary species were mainly Norway spruce (*Picea abies* (L.) H. Karst, 1881) and European beech (*Fagus sylvatica* L.). Most of the forest stands surrounding our study plots were managed for timber production. The plots were set up to reflect a gradient of dieback severity at the local scale; the dieback was measured in 2017 and was mainly induced by drought events over the last 30 years (Figs. S3–S5). In addition, local dieback conditions were cross-referenced with the empirical level of dieback in the landscape surrounding each study plot.

7.2.2 Beetle sampling, identification and characterisation

Saproxylic beetles were captured in two flight–interception traps per plot, each at least 20 m from the other, for a total of 112 traps in the 56 plots studied. Therefore, the traps were placed around the centre of each study plot. The traps consisted of a crossed pair of transparent plastic shields (40 \times 60 cm) above a funnel leading into a container filled with an unbaited preservative (50% propylene glycol and 50% water with detergent). The traps were hung roughly 1.5 m above the ground near the centre of the plot and were sampled every month from mid-May to mid-September 2017. All the saproxylic beetles collected were

identified to the highest possible taxonomic level (i.e. 83% at the species level, 2% at the genus level and 15% at the family level only (we retained the genera in which at least 100% of French species are known to be saproxylic, and families in which at least 75% of French species are known to be saproxylic), see Tab. S4; see Acknowledgments for the identifiers). We used the FRISBEE database to characterise species trophic guild at the larval stage (wood-eating, i.e. both xylo- and saproxylophagous species), substrate guild (cavicolous or fungicolous), and species rarity (rare vs. common) (Tab. 7.1; Bouget et al., 2005, 2019). We used genera and families only for global metrics, i.e. abundance and species richness of all saproxylic beetles.

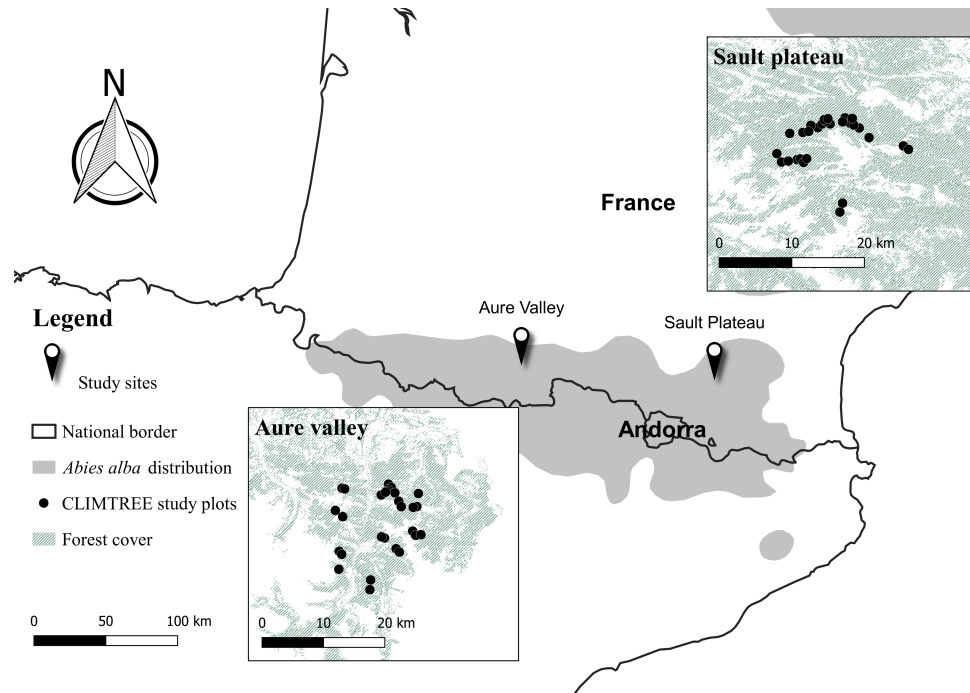


Figure 7.1 – Map of the study sites. Grey areas correspond to *Abies alba* distribution.

7.2.3 Monitoring forest dieback

Data acquisition

Colour infrared aerial photographs with a 1 m resolution were downloaded from the French National Geographical Institute (NGI) for our two study regions (<https://geoservices.ign.fr>). As NGI aerial photographs are taken approximately every 5 years, we looked for the past photographs closest to our insect sampling year (2017): photographs taken in 2016 for the Aure Valley and in 2015 for the Sault Plateau. We then extracted the forested areas from the colour infrared aerial photographs thanks to a land cover map based on Sentinel-2 images and deleted roads and paths (Inglada et al., 2017).

Machine learning process

We manually constructed vector training data through on-screen interpretation (Fig. 7.2c), resulting in 4256 polygons for four land cover classes: 1,743 polygons of dead crowns (41%), 1606 of living trees (37.7%), 212 of shady areas (5%), and 695 polygons of bare soil (e.g. meadows; 16.3%). We implemented a machine learning algorithm with the Orfeo Toolbox (OTB) software and we applied both a Pixel-based image analysis (PBIA) and an Object-based image analysis (OBIA) (Grizonnet et al., 2017).

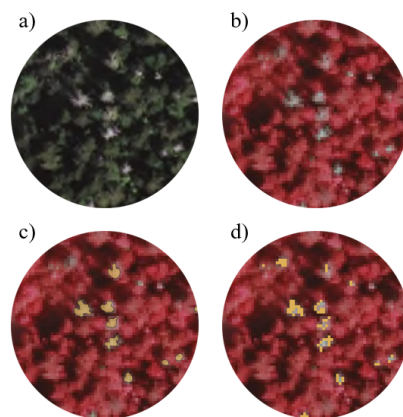


Figure 7.2 – Machine learning process: **a** natural colour (RGB) and **b** infrared colour (IRC) orthophotos of a forest composed of living and dead trees. Dead crowns are easily identifiable by their grey colour due to a lack of photosynthetic activity. We identified four types of polygons in a vector training layer (dead crowns, living trees, shady areas and bare soil—only dead crowns in **c**, to train a machine learning model with the random forest algorithm. **d** shows the result of the subsequent dead crown pixel classification in pale orange). All the images were taken from the centre point: lat. 488,182.46, lon. 6,205,612.67 (Lambert-93, EPSG:2154)

In the PBIA, we ran a Random Forest (RF) classification model (Breiman, 2001). RF is a widely used machine learning classification algorithm relying on a set of decision trees (Breiman, 2001; Immitzer et al., 2016). Fifty percent of the training vectors were used to train the classification model (proposed by default in the OTB) while the other fifty percent were used to validate the classification model.

In the OBIA, we performed segmentation on the colour infrared aerial photographs with the Large Scale Mean Shift method implemented in OTB (De Luca et al., 2019; Immitzer et al., 2016). We used a minimum size of four pixels (4 m²). As for the PBIA, we ran a RF model to classify the segmented vectors (Breiman, 2001; Immitzer et al., 2016).

In both approaches (PBIA and OBIA), we used the RF default setting values in OTB to train and classify the processes for optimal results (De Luca et al., 2019). Therefore, the maximum depth of the tree was set to 5, the maximum number of trees in the forest to 100 and the out-of-bag error was set to 0.01. The two RF classification models showed very similar accuracy results as measured by the Kappa index (PBIA: 0.72; OBIA: 0.68). Since OBIA does not facilitate dead crown classification compared to PBIA (see Immitzer et al., 2016 with tree species classification), we used only the results from the PBIA method, which requires less computer memory capacity (Grizonnet et al., 2017).

Measuring forest dieback at the landscape scale

We used our RF classification model with the PBIA approach to identify the dead crown pixels over large areas around our study plots. Our approach did not allow us to assess dead-tree density so we estimated the cumulative surface area of the dead and dying tree parts, i.e. the dead crowns (Larrieu et al., 2018). We then mapped and summed the dead crown pixels to assess a level of forest dieback over several spatial scales. We designated several nested buffer zones around our study plots in order to describe forest dieback along the gradient from the local to the landscape scale. The zones had radii of 25, 200, 500, 800, 1100 and 1500 m; we summed dead crown pixels in each of these buffer zones and we divided them by each buffer areas to assess a percentage of dead crown pixels (Tab. 7.1). Finally, for each buffer zone, we randomly selected non-overlapping buffers for the analysis, resulting for the 25

m buffer in 56 plots, 54 plots in the 200 m buffer, 35 plots in the 500 m buffer, 28 plots in the 800 m buffer, 25 plots in the 1100 m buffer, and 20 plots in the 1500 m buffer. We did not designate larger buffer zones to avoid further data degradation due to overlapping buffers. Hereafter, we designated the 25 m radius as describing local conditions, the 200 m radius as intermediate landscape and the larger radius as landscape-scale conditions (Fig. S7.7).

Table 7.1 – Overview of the predictors and response variables used in our study.

Variable	Definition	Mean \pm CI95%	Range (min-max)
Predictors			
<i>Forest dieback severity</i>			
25 m-scale	Percentage of DCP within the 25 m radius	3 \pm 1.2	0–19
200 m-scale	Percentage of DCP within the 200 m radius	2.4 \pm 0.9	0.01–11.1
500 m-scale	Percentage of DCP within the 500 m radius	2.1 \pm 1.01	0.02–10.4
800 m-scale	Percentage of DCP within the 800 m radius	1.98 \pm 1.02	0.02–8.7
1100 m-scale	Percentage of DCP within the 1100 m radius	1.7 \pm 0.96	0.02–7.2
1500 m-scale	Percentage of DCP within the 1500 m radius	1.9 \pm 1.17	0.02–7.4
Responses			
<i>All species</i>			
Abundance	Abundance of all saproxylic beetles	820 \pm 142	179–3052
Richness	Species richness of all saproxylic beetles	83 \pm 4	51–123
<i>Common species</i>			
Abundance	Abundance of common saproxylic beetles	715 \pm 122	120–2716
Richness	Species richness of common saproxylic beetles	70 \pm 4	43–105
<i>Rare species</i>			
Abundance	Abundance of rare saproxylic beetles	22 \pm 9	3–245
Richness	Species richness of rare saproxylic beetles	6 \pm 0.5	2–11
<i>Wood-eating species</i>			
Abundance	Abundance of wood-eating beetles	548 \pm 119	104–2589
Richness	Species richness of wood-eating beetles	31 \pm 2	16–50
<i>Cavicolous species</i>			
Abundance	Abundance of cavicolous beetles	50 \pm 8	8–143
Richness	Species richness of cavicolous beetles	11 \pm 1	3–21
<i>Fungicolous species</i>			
Abundance	Abundance of fungicolous beetles	242 \pm 29	41–622
Richness	Species richness of fungicolous beetles	33 \pm 2	17–47
<i>Phylogenetic diversity</i>			
SES faith's	PD Faith's standardized phylogenetic diversity	-1.35 \pm 0.2	-3.0 to 0.2
Variability	Phylogenetic species variability	0.9 \pm 0.002	0.88–0.91
Evenness	Phylogenetic species evenness	0.78 \pm 0.03	0.35–0.87
<i>Functional diversity (Mouillot et al., 2013; Villéger et al., 2008)</i>			
Richness	Functional richness	44 \pm 2	28–67
Divergence	Functional divergence	0.81 \pm 0.02	0.63–0.94
Evenness	Functional evenness	0.59 \pm 0.01	0.51–0.67
<i>Community weighted mean (CWM)</i>			
DW diameter	Mean trait value of deadwood diameter preference	2.23 \pm 0.03	1.96–2.49
DW decay	Mean trait value of deadwood decay preference	2.48 \pm 0.07	2.1–3.14
Canopy closure	Mean trait value of canopy-closure preference	1.68 \pm 0.02	1.39–1.87
Body size	Mean trait value of body size	4.9 \pm 0.4	2.9–9.9
<i>Functional dispersion (FDis)</i>			
DW diameter	Trait variance of deadwood diameter preference	0.54 \pm 0.04	0.28–0.98
DW decay	Trait variance of deadwood decay preference	0.7 \pm 0.05	0.26–0.95
Canopy closure	Trait variance of canopy-closure preference	0.75 \pm 0.04	0.39–1.2
Body size	Trait variance of body size	0.73 \pm 0.08	0.24–0.32

DCP = dead crown pixels, CWM = community-weighted means, FDis = functional dispersion, DW = deadwood rare species = patrimonial value ≥ 3 in France

7.2.4 Statistical analysis

Data analysis was conducted with R software 4.0.0 (R Core Team, 2022). Firstly, we pooled the two traps from each plot and calculated abundance and species richness for the substrate and trophic beetle guilds. We also calculated abundance and species richness for both common and rare saproxylic beetle species as well as the total abundance and species richness. Furthermore, to account for missing data, we incorporated the log coefficient based on the number of undisturbed sampling months weighted by monthly arthropod abundance into all models as an offset (trap sometimes destroyed).

Secondly, to assess functional diversity indices for the community, we extracted quantitative values for preferred deadwood diameter and decay level for larval development, canopy openness preference, and mean body size for each of the captured saproxylic beetle species, as in (Gossner et al., 2013; Janssen et al., 2017). For each plot, we calculated two multidimensional indices: community-level weighted means (CWM) and functional dispersion (FDIs), defined as the mean and dispersion of the trait values weighted by the relative abundance of each species according to their values of quantitative functional traits (Tab. 7.1; dbFD function, FD R-package; Laliberté et al., 2014). In addition, we calculated the three functional diversity indices proposed by Villéger et al. (2008) based on four quantitative functional traits (i.e. preferences in deadwood diameter and decay and canopy openness, and mean body size) (Tab. 7.1): (i) functional richness (FRic), i.e. "the range of functional space filled by the community"; (ii) functional divergence (FDiv), which "relates to how abundance is distributed within the volume of functional trait space occupied by the community"; and (iii) functional evenness (FEve) or "the evenness of abundance distribution in a functional trait space" (Villéger et al., 2008). These three indices should be able to quantify the functional changes occurring in a community after a disturbance (Mouillot et al., 2013).

Thirdly, we calculated Faith's standardized phylogenetic diversity index (SES Faith's PD) to obviate the relationship between Faith's PD and species richness (Pearson's $r = 0.98$, $P < 0.001$). We also calculated two phylogenetic species-diversity metrics: phylogenetic species variability (PSV) and evenness (PSE). PSV "is one when all species are unrelated and approaches zero as species become more related"; PSE "is one when species abundances are equal and species phylogeny is a star" (Tab. 7.1; Kembel et al., 2020). DNA barcode consensus were mined from the BOLD data system (Ratnasingham and Hebert, 2007) whenever accessible for each saproxylic beetle species morphologically identified. When multiple records and BINs (Ratnasingham and Hebert, 8 juil. 2013) were available for a given species, a choice was made according first to geographic area of sampling, and second to sequence length and quality. Close geographical areas were favoured as were high-quality 658 bp-long sequences ($N < 1\%$) whenever possible. A total of 349 species out of 393 (88.8%) beetle species collected had DNA barcodes available. The dataset of the records we used for phylogenetic diversity is publicly available at the following <https://doi.org/10.5883/DS-PHYLOCOL>. COI consensus were first aligned with BOLD aligner to check for sequence quality and validity. Trimming of longer or misaligned consensus was manually applied whenever necessary. Final sequence alignment was performed in MUSCLE 3.8.425 (Edgar, 2004) with 8 iterations and a maximum-likelihood phylogenetic tree was constructed with a general time-reversible (GTR) model and 500 bootstrap iterations in FastTree ver. 2.1.11 (Price et al., 2010). In order to compare phylogenetic diversity among different dieback levels, an unrooted tree was preferred (Nipperess and Matsen, 2013). With picante package ver. 1.8.2 (Kembel et al., 2020), we pruned the species present across all our study regions and plotted phylogenetic trees for each study plot. We calculated the respective standardized PD, PSV and PSE values for each plot with the "ses.pd" and "psd" functions (picante R-package).

To deal with the over-dispersion of count variables (Bates et al., 2020), we used the glmmTMB R-package (Magnusson et al., 2020) to run Generalized Linear Mixed Models (GLMMs) with "region" (i.e. Aure Valley or Sault Plateau) as a random variable. In addition, to better include the differences between the two regions in the models, we also added the proportion of fir trees in the surrounding

forests, in an area of 700 ha, as a fixed effect (see section 7.2). Response variables were the abundance and species richness for each guild of saproxylic beetles, the functional-trait variables (i.e. CWM and FDis for each quantitative functional trait, and FRic, FDiv and FEve for overall functional diversity), and the phylogenetic diversity indices (i.e. SES Faith's PD, PSV and PSE). We implemented both simple and multiple regressions. The simple regressions, hereafter referred as **univariate models**, were composed of the random variable (i.e. region), proportion of fir trees in the 700 ha area as a fixed co-variable, the offset to account for missing data, and the percentage of dead crown pixels for a particular spatial scale as a predictor. For each response variable, we selected the best-fitting error structure with the `fitdist` function from the `fitdistrplus` R-package (Delignette-Muller et al., 2019). Then, we selected the best relationship structure for each response variable and predictor variable (i.e. by comparing the Akaike Information Criterion for small sample sizes (AICc) between linear and logarithmic regressions). Since six different spatial scales were compared (R = 25 m, 200 m, 500 m, 800 m, 1100 m and 1500 m), we applied a Post-Hoc Holm adjustment of p-values ("`p.adjust`" function). Finally, we extracted estimates (i.e. β -coefficients) and adjusted p-values from each `glmmTMB` model. We used estimate values to select the best landscape scale for each tested response variable.

We then performed multiple regressions with generalized linear mixed models with "region" (Aure Valley or Sault Plateau) as a random variable and including as fixed variables, the measure of local dieback and the best landscape scale, proportion of fir trees in the 700 ha areas as co-variable, and the offset to account for missing data. We checked for non-collinearity between fixed variables, with the "`check_collinearity`" function from the `performance` R-package (Lüdtke et al., 2020) and always observed a variance inflation factor (VIF) below three. As three different terms in the multiplicative models were involved, we performed Post-Hoc Holm adjustments on each of their p-values. Our purpose was to evaluate the potential interactive effect between the local (25 m) and the most appropriate landscape scale (i.e. the landscape scale with the highest β -coefficient and/or highest significance) with a multiplicative interaction model (Eq. 7.1). Since the 200 m scale was highly correlated with the 25 m-scale (Pearson's $r = 0.78$, $P < 0.001$), we excluded this metric from our analysis (Fig. ??, Tab. S7.1).

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_{12} X_1 X_2 + \varepsilon \quad (7.1)$$

which is the multiplicative equation assessing whether there is an interactive relationship between X_1 and X_2 . X_1 = severity of local dieback; X_2 = severity of most suitable landscape dieback; β_1 and β_2 = model coefficients for both forest dieback metrics (local and landscape); β_{12} = coefficient for the interaction term $X_1 X_2$; ε = model residuals.

In multiplicative interaction models, hereafter referred to as "**multiplicative models**", β_1 and β_2 are significantly different from zero when X_1 and X_2 are respectively equal to zero ($H_1: \beta_1 \neq 0$ when $X_2 = 0$ and vice-versa) (Braumoeller, 2004). We associated the results of the multiplicative models with the ecological mechanisms affecting the spatial pattern of the saproxylic beetles. When $H_1: \beta_1 \neq 0$ could not be rejected, we hypothesised an effect of local resource concentration since we were assessing the effect of local forest dieback on saproxylic beetles in the case of limited dieback at the landscape scale (Fig. 7.3a). When $H_2: \beta_2 \neq 0$ could not be rejected, we hypothesised a spill-over effect since we were assessing the effect of forest dieback at the landscape scale in the case of limited local dieback (Fig. 7.3b). We hypothesised that a significantly positive interaction term (β_{12}) reflected a synergistic/amplifying effect (Fig. 7.3c) and that a significantly negative interaction term would support a dilutive/saturated effect and the habitat-patch hypothesis (Fig. 7.3d; Fahrig, 2013; Seibold et al., 2017). Furthermore, we assumed that a significant response to local forest dieback in the univariate model but not in the multiplicative model and/or a significant response to landscape dieback in the univariate model but not in the multiplicative model would both support the additional importance of both scales to describe local saproxylic beetle assemblages (i.e. the habitat-amount hypothesis; Fig. 7.3e; Fahrig, 2013; Seibold et al., 2017). Indeed,

cancelling univariate significant effects in multiplicative models indicates that the level of forest dieback, i.e. the amount of dieback-induced resources, matters at both local and surrounding landscape scales and not just at one particular scale. In addition, the absence of an interaction effect would also support the habitat-amount hypothesis (Fahrig, 2013; MacArthur and Wilson, 1967; Seibold et al., 2017).

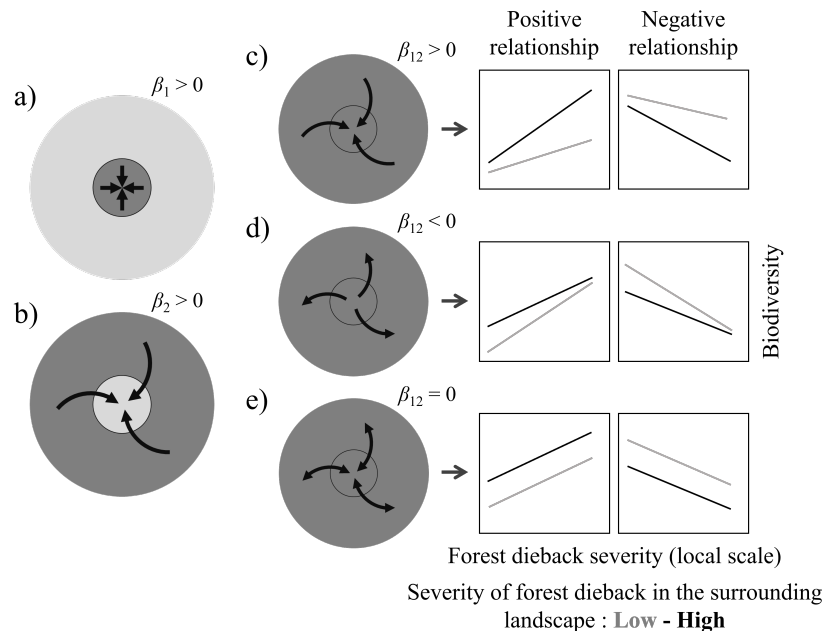


Figure 7.3 – Hypothesised saproxylic beetle responses to the terms of the multiplicative interaction models (inner circle = local conditions (associated estimates = β_1); outer circle = landscape conditions (associated estimates = β_2); light grey = healthy forest area; dark grey = disturbed forests; arrows represent species fluxes) (a and b describe simple terms effects while c–e describe interactive term). a $\beta_1 > 0$ = concentration effect; b $\beta_2 > 0$ = spill-over effect; c $\beta_{12} > 0$ = synergistic effect; d $\beta_{12} < 0$ = dilution or habitat-patch effect; e $\beta_{12} = 0$ = habitat-amount hypothesis. Moreover, if there is a significant local effect in the univariate model but not in the multiplicative model, or a significant landscape effect in the univariate model but not in the multiplicative model, it supports that local and landscape conditions act additionally.

7.3 Results

Our final dataset comprised 50,067 specimens of 393 saproxylic beetle species belonging to 50 families. The range of species richness was 51–123 species/plot with an average of 83 ± 4 species/plot (CI 95%; Tab. 7.1).

7.3.1 Validation of forest dieback metrics

To assess the relevance of the percentage of dead crown pixels as an indicator of forest dieback, we evaluated the accuracy of the relationship between the local sum of dead crown pixels ($R = 25$ m) and field measurements of forest dieback carried out according to the ARCHI protocol. The ARCHI protocol classifies trees in a gradient from healthy to dead, based on their architecture. In our study, we applied the protocol to the 20 fir trees closest to each plot centre. It resulted in a standardised measure of dieback at plot scale according to a hypothetical lower (all 20 trees are healthy) and higher (all 20 trees are dead) values of dieback (i.e. standardised mean dieback of 39% ($\pm 3\%$ CI95%), minimum value at 9% and maximum at 59%). We observed a significant relationship between the two variables (β -Estimate = 0.7; P

< 0.01; Fig. S7.5), which indicates that our classification model of dead crown pixels and the percentage of these pixels provided a consistently accurate description of the local forest dieback assessed on site. In addition, we validated our landscape-scale estimates of forest dieback by cross-checking the relationship between the percentage of dead crown pixels at the landscape scales (i.e. R = 200 to 1500 m) with the European disturbance map edited by Senf and Seidl (2021a; 2021b), which is based on a time series analysis of the spectral band values of Landsat satellite photographs ($P < 0.001$; Fig. S7.6).

7.3.2 Relationship among taxonomic, phylogenetic and functional diversity

We did not observe a relationship between total saproxylic beetle species richness and the phylogenetic diversity metrics (Fig. S7.1). Nevertheless, we found a positive relationship between total species richness and FRic (Fig. S7.1), but not with FDiv (Fig. S7.1) and FEve (Fig. S7.1). We did not observe any relationship between the phylogenetic diversity metrics and FRic, though there was a significantly negative relationship between PSE and FDiv (Fig. S7.1) and a positive relationship between PSE and FEve (Fig. S7.1).

7.3.3 Response of taxonomic diversity to dieback

General metrics

In the univariate models, both local and landscape dieback metrics had positive effects on abundance and richness of total and common species, abundance and richness of common species, and on abundance of rare species (Fig. 7.4a). In contrast, rare species richness did not respond to forest dieback at any scale (Fig. 7.4a). For abundances, scales of effect were detected at the local scale, whereas for species richness, scales of effect were detected at 200 m scale (Fig. 7.4a). No effect was detected in the multiplicative models (Tab. 7.2).

Feeding and substrate guilds

In the univariate models, the abundance of wood-eating species was positively affected by local forest dieback only (i.e. the scale of effect; Fig. 7.4e). In contrast, the richness of wood-eating species positively responded to both local- and landscape-scale dieback (with higher scale of effect at 200 m scale; Fig. 7.4e). Still in the univariate models, abundance of cavicolous species positively responded to landscape scales (200 m and 1500 m scales; Fig. 7.4e), while richness positively responded to both local and intermediate landscape scales (i.e. 25 m and 200 m; Fig. 7.4e). Nevertheless, they both had scale of effect at 200 m scale (Fig. 7.4e). In the univariate models, fungicolous species abundance responded positively to forest dieback at the local and landscape scales (with high scales of effect at 200, 800, and 1100 m scales), while richness was only affected by the 200 m scale (Fig. 7.4e). In the multiplicative models, neither the abundance nor the species richness of wood-eating, cavicolous, and fungicolous beetles significantly responded to forest dieback (Tab. S2).

7.3.4 Response of phylogenetic diversity to dieback

In the univariate models, we only observed negative response of phylogenetic evenness to forest dieback at the 1100 m scale (Fig. 7.4b). Otherwise, in the multiplicative models, we detected significant responses of standardized Faith's index of phylogenetic diversity: positively to both simple effects (i.e. local and landscape dieback), and negatively to the interactive effect (Tab. 7.2).

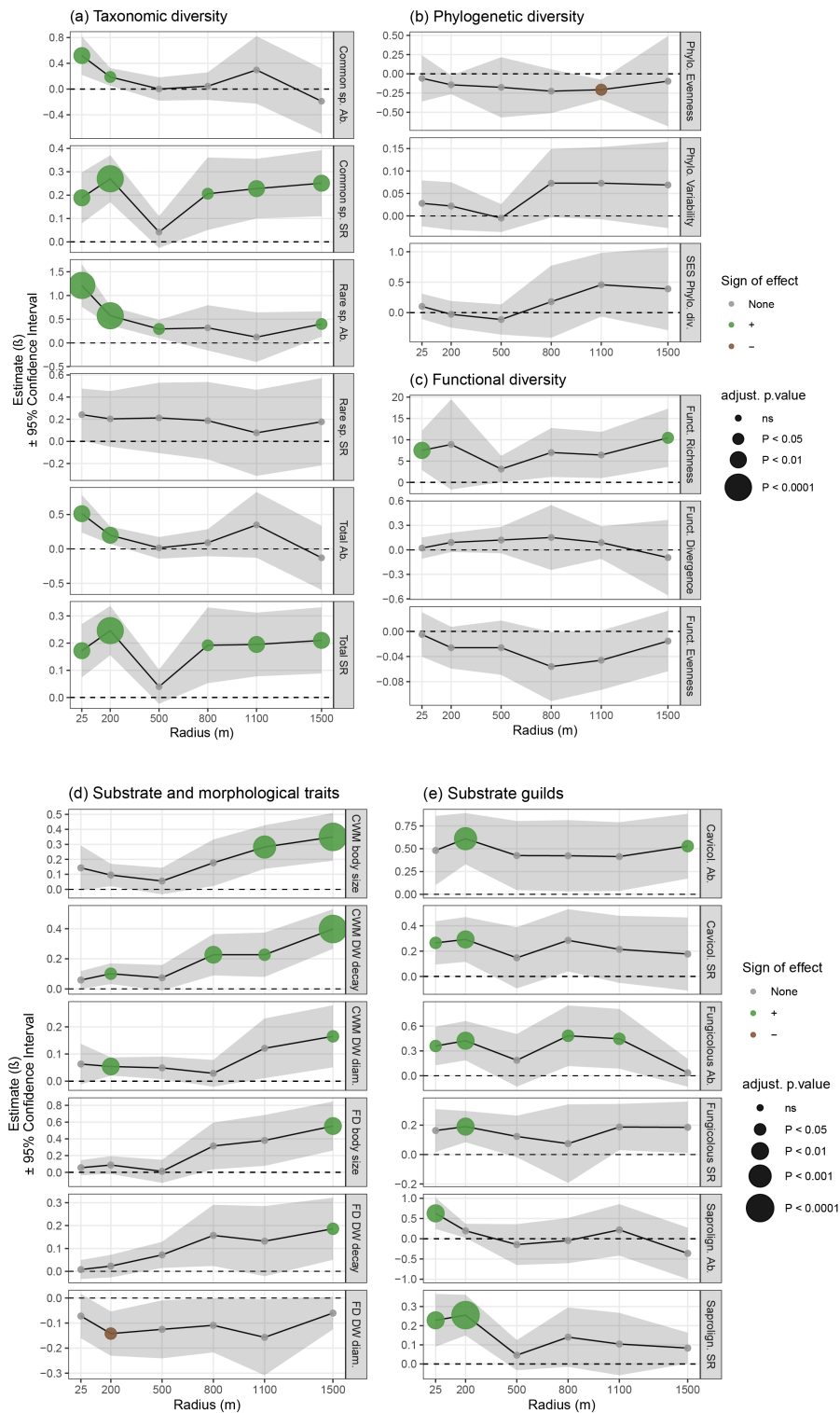


Figure 7.4 – Response of local general saproxylic beetle assemblages to dieback severity measured over different spatial scales (a taxonomic diversity; b phylogenetic diversity; c functional diversity; d substrate traits; e substrate guilds). Coloured circles indicate β -estimates from the univariate glmmTMB models; their diameter varies with adjusted p value. The shaded grey area indicates the 95% confidence interval of each β -estimate. "DW" = "deadwood"

7.3.5 Response of functional diversity to dieback

In the univariate models, we only observed positive effects of both local and landscape forest dieback on FRic (Fig. 7.4c). Concerning substrate and morphological metrics, we noted positive effects of forest dieback on the mean community preference for deadwood diameter (CWM DW diam.), for deadwood decay (CWM DW decay), and for body size (CWM body size) at the landscape scale (higher scales of effect at 1500 m scale; Fig. 7.4d). We observed parallel negative effects for forest dieback at the landscape scale on the functional dispersion of deadwood diameter preference (at 200 m scale; FD DW diam.; Fig. 7.4d) and positive effects, also at the landscape scale, on the functional dispersion of deadwood decay preference (FD DW decay) and body size (FD body size; scale of effect at 1500 m scale; Fig. 7.4d). In the multiplicative models, we did not observe any significant responses of functional metrics to forest dieback (Tab. 7.2). Finally, the functional traits canopy opening preference did not respond to forest dieback in either the univariate or multiplicative models (Tab. S2).

7.4 Discussion

7.4.1 Overall forest dieback effect

Given the scale of the expected increase in the frequency and spatial extent of forest dieback and decline in the future, assessing their current and long-term consequences on forest communities is paramount (e.g., [Anderegg et al., 2013](#); [McDowell et al., 2020](#); [Sallé et al., 2021](#)). As expected, we showed that the intensity of forest dieback positively affected the taxonomic diversity of saproxylic beetles, differently at the local and landscape scale (Fig. 7.4). This probably results from the accumulation of deadwood and tree-related microhabitats associated with increased canopy openness, since both environmental factors generally have positive effects on the species richness and abundance of saproxylic beetles ([Bouget et al., 2014a](#); [Godeau et al., 2020](#); [Müller and Büttler, 2010](#); [Sallé et al., 2020, 2021](#)).

7.4.2 Local- and large-scale effects of forest dieback

Many species of saproxylic beetle are considered highly mobile and therefore only slightly dispersal-limited; they therefore potentially respond to large scales of effect ([Jackson and Fahrig, 2015](#); [Janssen et al., 2016](#); [Thorn et al., 2018b](#)). Indeed, they may cover long distances, within a limit of roughly ≤ 10 km ([Komonen and Müller, 2018](#)), to find suitable habitats and/or resources (related to the deadwood size, decay stage, tree species and position; to tree-related microhabitats; or to the presence of open areas; [Grove, 2002](#); [Stokland et al., 2012](#)). Our results highlight the relevance of the landscape scale (i.e. in this study, from 200 to 1500 m) when considering the effect of forest dieback on local saproxylic beetle assemblages. Despite strong correlation with the local scale, we noticed that the 200 m scale could be considered as the scale of effect for species richness of most guilds of saproxylic beetles. In an experimental test of the habitat-amount hypothesis, [Seibold et al. \(2017\)](#) showed that the scales of effect for species richness of saproxylic beetles were about 40 to 120 m depending on the group, which is approximately in line with our results. However, we lack resolution along our buffer gradient and therefore the actual scale of effect is certainly another value close to our result. In contrast, the abundance of all species as well as common, rare, and wood-eating species responded mainly to local forest dieback (Fig. 7.4). Consequently, species richness and abundance responded differently to forest dieback and should therefore be determined by distinct mechanisms: abundance seems to be mainly driven by patch size while species richness seems to be mainly driven by the local landscape. It has already been shown in previous studies that the accumulation of deadwood, both at local and landscape scales, has positive effects on saproxylic beetles ([Franc et al., 2007](#); [Gibb et al., 2006](#); [Haeler et al., 2021](#); [Økland et al., 1996](#); [Sverdrup-Thygeson et al., 2014](#)). Likewise, local canopy openings as well as an interconnection within the landscape forest matrix of fine patches of open habitats, i.e. gaps, is also beneficial to saproxylic

beetle biodiversity (Bouget and Duelli, 2004; Bouget et al., 2014a; Kozel et al., 2021; Seibold et al., 2016).

Table 7.2 – Results from the multiplicative interaction models of the effects of local ($R=25$ m) and surrounding landscape (highest scale of effect) dieback on the taxonomic, phylogenetical, and functional diversity of saproxylic beetles.

Responses of local assemblages metrics	Models Metrics	Description df	R ²	Simple effects β coeff.	Interactive effects β coeff.
Taxonomic diversity					
Abundance (All)	Local	23	0.18	0.5 ^{ns}	-0.03 ^{ns}
	Landscape 1100m			-0.3 ^{ns}	
Richness (All)	Local	18	0.37	0.2 ^{ns}	-0.16 ^{ns}
	Landscape 1500m			0.23 ^{ns}	
Phylogenetical diversity					
SES Faith's PD	Local	18	0.21	0.63*	-0.9*
	Landscape 1500m			1.33*	
Variability	Local	26	0.32	0.11 ^{ns}	-0.06 ^{ns}
	Landscape 800m			0.06 ^{ns}	
Evenness	Local	23	0.31	0.16 ^{ns}	-0.08 ^{ns}
	Landscape 1100m			-0.18 ^{ns}	
Functional diversity					
Richness	Local	18	0.32	4.4 ^{ns}	6.3 ^{ns}
	Landscape 1500m			0.59 ^{ns}	
Divergence	Local	26	0.28	0.3 ^{ns}	-0.76 ^{ns}
	Landscape 800m			0.66 ^{ns}	
Evenness	Local	26	0.32	-0.02 ^{ns}	0.03 ^{ns}
	Landscape 800m			-0.07 ^{ns}	

* Effects were tested with generalized linear mixed models (with "region" as a random variable and proportion of fir trees in landscape as fixed co-variable). Values shown are β -estimates from glmmTMB models. Colours represent the direction of the effect: green for a positive effect of dieback on the considered variable, red for negative effect, and grey when no significant effects were detected. "df" = "degrees of freedom", "R²" = "R-squared" (since there is no method to calculate R² from glmmTMB model, values are derived from glm.nb and glm models). See Tab. S1 and S2 for all response variables. ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

In addition, we observed a significant landscape effect of forest dieback on the abundance of both cavicolous and fungicolous species (Fig. 7.4e). This result suggest that forest dieback does not just increase deadwood amount and canopy openness but also favours the development of tree-related microhabitats such as the fruiting bodies of saproxylic fungi and cavities (e.g., rot-holes; Larrieu et al., 2018; Ojeda et al., 2007; Speckens, 2021; see chapter 4).

We did not observe any significant interaction between local and landscape forest dieback for metrics of taxonomic diversity (Tab. 7.2). According to Seibold et al. (2017), the lack of interaction between these two spatial scales could support the habitat-amount hypothesis since the amount of habitat at both scales is merely additive (Fig. 7.3). This is further supported by the fact that local and landscape effects alone cancelled each other out in our multiplicative models, while most of the univariate-model effects for taxonomic diversity were significant (Fig. 7.4; Tab. 7.2). The habitat-amount hypothesis predicts that "species richness in a sample site is independent of the area of the particular patch in which the sample site is located (its local patch)" (Fahrig, 2013). Therefore, in our study, local scale alone (i.e. without any dieback areas in landscape) should not have been sufficient to detect dieback effects on saproxylic beetle biodiversity, even if it appears as the potentially scale of effect. Nevertheless, the opposite is also true: forest dieback surrounding an undisturbed forest patch cannot contribute to local biodiversity, since the habitat or resource of interest is not locally present (Tab. 7.2). Nevertheless, and despite the non-collinearity in the models (VIF < 3), local and landscape conditions of forest dieback were correlated

(Tab. S7.1) and thus, the cancellation of significant effects in the univariate models could also be the result of statistical artifacts and further research is needed.

Forest dieback at the landscape scale also had effects on the functional diversity metrics, mainly substrate and morphological traits (CWM and FDis) which did not respond to local forest dieback (Fig. 7.4d). In another study, based on data from the same Pyrenean plots and from plots located in Bavarian montane forests (Cours et al., 2021; see chapter 5), we hypothesised that the severity of the local forest dieback in Bavaria was correlated to forest dieback severity at the landscape scale, as sudden, large-scale tree mortality occurred in the area following a major bark beetle outbreak (mean bark beetle gap size = 6.8 ha; Müller et al., 2008). In contrast, the drought-induced dieback in the Pyrenean forests caused gradual mortality in discrete patches across the landscape; in this case, the local conditions did not necessarily reflect large-scale conditions (Andrew et al., 2016; Cours et al., 2021). These variations in the immediacy and scale-intensity of the dieback may explain (i) why the local forest dieback in the Pyrenean mountains did not affect functional trait metrics in our previous study (Cours et al., 2021), and (ii) why, in this study, the same metrics only responded to landscape-scale conditions. Our results therefore suggest that studying local conditions alone may be insufficient to detect the functional response of saproxylic beetles to forest dieback when tree mortality occurs in discrete patches, and that landscape conditions can act as a strong filter on trait diversity (Fig. 7.4d; Cours et al., 2021; Gámez-Virués et al., 2015).

7.4.3 Contrasting responses of different biodiversity dimensions to forest dieback

While taxonomic diversity was affected primarily by local and intermediate-landscape forest dieback (and secondarily by larger landscape scales), it appears from our results that functional diversity, through substrate and morphological traits, responded primarily to forest dieback at the largest landscape scale (i.e. 1500 m; Fig. 7.4d). In parallel, functional richness responded positively at the local scale and at the 1500 m scale (Fig. 4c). Furthermore, forest dieback only affected phylogenetic diversity through evenness, at the 1100 m scale (Fig. 7.4b). In contrast, standardized Faith's phylogenetic index (ses.PD) was the only one response variable that significantly responded to local and landscape forest dieback in the multiplicative model (Tab. 7.2). From this multiplicative model, it seems that the spatial pattern of dieback was important for the ses.PD. Indeed, spatial patterns mixing areas of forest dieback with undisturbed areas seem to lead to higher phylogenetic index values than randomly expected (i.e. phylogenetic overdispersion; Webb and Pitman, 2002).

Consequently, the diversity and quantity of habitats and resources released by forest dieback (i.e. deadwood, tree-related microhabitats and canopy openness) increased abundance and species richness of saproxylic beetles, and lead to more heterogeneous functional assemblages, as suggested by the more-individuals and the habitat-heterogeneity hypotheses (Seibold et al., 2016). Similarly, the increase in spatial heterogeneity due to the mixing of declining and undisturbed forests had a positive effect on phylogenetic diversity. For example, Kozák et al. (2021) showed that phylogenetic diversity of saproxylic beetles was positively affected by canopy openness, which in turn was positively influenced by recent disturbances.

7.4.4 Functional responses of assemblages to forest dieback: heterogenisation and specialisation

Forest dieback increased beetle functional richness (FRic), at both local and landscape scales (Fig. 7.4c). In our study, the increase in total species richness seemed to be associated with this increase in FRic. This indicates that the range of functional traits is quite broad in the functional space of disturbed stands and within disturbed landscapes; in other words, functional traits have more extreme values in declining forests (Mouillot et al., 2013). This is congruent with previous observations showing that the functional richness of saproxylic beetle assemblages is positively influenced by the local amount and

diversity of deadwood, as well as by canopy openness (local = 0.1 ha, $R \approx 18$ m; [Thorn et al., 2018b](#)), features which are typically favoured during forest decline and dieback ([Cours et al., 2021](#); [Sallé et al., 2021](#); [Thorn et al., 2018b](#)). Here, we demonstrate that this probably stands true at larger spatial scales.

In addition, we observed functional specialisation in species preference for deadwood diameter: when forest dieback increased at the landscape scale, local assemblages preferred larger deadwood and functional dispersion was lower (CWM and FDis Diameter; Fig. 7.4d). A previous study showed that the functional specialisation of saproxylic beetles towards large-diameter and well-decayed deadwood occurs when the overall amount of deadwood increases ([Gossner et al., 2013](#)). This functional specialisation might not account for the needs of species that prefer small-diameter deadwood. Nevertheless, these species still benefit from a relatively high amount of deadwood and are also less sensitive to intense forest management in the surrounding area ([Gossner et al., 2013](#)). Moreover, we observed that forest dieback at the landscape scale led to an increased preference of the saproxylic beetle assemblages for more decayed deadwood, along with a higher functional dispersion than in healthy forests (CWM and FDis Decay; Fig. 7.4d). Therefore, our results suggest that iterative forest dieback events had released a large amount of large-diameter deadwood in varying stages of decay, which is of great value for biodiversity ([Bouget et al., 2013](#); [Gossner et al., 2013](#); [Kozák et al., 2021](#); [Lachat et al., 2013](#); [Similä et al., 2003](#)). Finally, our results showed that increasing forest dieback at the landscape scale lead to increasing mean body size of local saproxylic beetle assemblages, with higher trait dispersion (Fig. 7.4d). It means that forest dieback occurring over large areas favoured larger beetle species. Large saproxylic beetle species, preferring larger deadwood pieces are known to be the most threatened across the European forests ([Hagge et al., 2021](#); [Seibold et al., 2015](#)). As a result, forest dieback could benefit threatened species in commercial forests.

Intensive management generally leads to functional homogenisation, which is often driven by the decline of specialist species in favour of generalists ([Clavel et al., 2011](#)). Our study plots were managed, and we found that forest dieback induced functional heterogenisation with an increase in the mean and dispersion of most of the traits tested. We hypothesise that the functional heterogenisation was driven by the high resource availability and habitat diversification subsequent to the forest dieback. At the landscape scale, the dieback logically resulted in a matrix of remaining live trees, acting as disturbance refugia ([Krawchuk et al., 2020](#)), and discrete patches of open woodlands with standing dead trees and snags, logs, large deadwood, tree-related microhabitats, etc. Ultimately, this promoted the coexistence of a wide variety of ecological niches ([Swanson et al., 2011](#)), allowing the co-occurrence of functionally diverse saproxylic beetle assemblages ([Kozák et al., 2021](#); [Thorn et al., 2018b](#)).

7.4.5 Application and conclusions

Our study revealed that the taxonomic, functional and phylogenetic diversity of saproxylic beetle assemblages in Pyrenean montane fir forests significantly benefitted from forest dieback, at both local and landscape scales, mainly thanks to landscape heterogenisation, to a large build-up of deadwood and to more canopy openings ([Bouget et al., 2014a](#); [Sallé and Bouget, 2020](#); [Sallé et al., 2020](#); [Thorn et al., 2017, 2018b](#)). Our results lead us to consider unharvested declining forest stands as potentially relevant sites for biological conservation ([Hlásny et al., 2021a](#); [Müller et al., 2010](#)) because they favour the functional diversity, abundance and richness of saproxylic beetle species otherwise threatened in conventionally managed stands ([Grove, 2002](#); [Hagge et al., 2021](#); [Seibold et al., 2015](#)). Moreover, it seems that local clusters of forest dieback alone may be insufficient to maintain diverse communities of saproxylic beetles. It is also necessary to maintain areas of forest dieback in the landscape, i.e. at scales of at least 1100 m and 1500 m (Fig. 7.4; Tab. 7.2), mainly for functional diversity. Furthermore, the discrepancies we found in the response of various biodiversity dimensions call for a multidisciplinary integrative approach and studies on wide species communities in disturbed forests ([Sallé and Bouget, 2020](#); [Sallé et al., 2021](#); [Sire et al., 2022](#)).

7.5 Supplementary material

Supplementary materials for this chapter can be found in appendix [E](#).

Part V

Consequences of human intervention following forest dieback on ecosystem resilience

Conséquences des coupes sanitaires sur la résilience des écosystèmes forestiers perturbés - une revue de la littérature

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Abstract

Traditionally, salvage and sanitation logging has been the response of forest managers to forest dieback in an attempt to limit its economic impact. In this literature review, we analyse the consequences of sanitary logging on the resilience of forest ecosystems. It appears that sanitary logging affects forest species communities, eliminating species from mature forests and promoting those from young stands. They do not have a strong effect on tree regeneration, but dryland species and species with obligatory sexual regeneration seem to be disadvantaged. Salvage logging has no effect on future forest fires but increases the risk in the short term. In addition, the physico-chemical characteristics of soils are affected: compaction, reduced fertility and lower carbon storage. We invite managers to adopt an integrative and adaptive management approach.

Keywords: Forest dieback, Sanitation logging, Biodiversity, Integrative management, Adaptive management, Natural disturbances

Résumé

Traditionnellement, la coupe dite "sanitaire" est la réponse apportée par les gestionnaires au dépérissement forestier pour tenter de limiter son impact économique. Nous analysons dans cette revue de littérature les conséquences des coupes sanitaires sur la résilience des écosystèmes forestiers. Il apparaît que les coupes sanitaires affectent les communautés d'espèces forestières, en éliminant les espèces de forêts matures et en promouvant celles de jeunes peuplements. Elles n'ont pas d'effet fort sur la régénération des arbres mais les essences dryades et à régénération sexuée obligatoire semblent défavorisées. Les coupes sanitaires n'ont pas d'effet sur les futurs incendies de forêts mais augmente tout de même le risque à court terme. Par ailleurs, les caractéristiques physico-chimiques des sols sont affectées : tassement, baisse de fertilité et moindre stockage de carbone. Nous invitons les gestionnaires à adopter une approche de gestion à la fois intégrative et adaptative.

Mots-clés : Dépérissement forestier, Coupe sanitaire, Biodiversité, Gestion intégrative, Gestion adaptative, Perturbations naturelles

8.1 Introduction

Les émissions de gaz à effet de serre, depuis le début de l'ère industrielle, ont conduit aujourd'hui à une augmentation globale des températures. Ce changement climatique d'origine anthropique a pour conséquence de modifier les régimes de perturbations naturelles, qu'elles soient biotiques ou abiotiques (Seidl et al., 2017; Senf and Seidl, 2021b). Il est notamment observé et attendu une augmentation de la fréquence, de l'intensité et de l'étendue spatiale des sécheresses en Europe (Allen et al., 2010; Samaniego et al., 2018). Depuis une trentaine d'années, les changements liés aux différents régimes de sécheresse en Europe ont pour conséquence une augmentation de la mortalité des arbres et donc des peuplements forestiers (Senf et al., 2020; Taccoen et al., 2019, 2022). Il est notamment observé un phénomène d'accélération de l'importance de ces sécheresses ces dix dernières années (Moravec et al., 2021; Senf and Seidl, 2021b). Ces changements de régime de perturbation peuvent aboutir à des phénomènes de dépérissement complexes. La succession dans le temps de différents facteurs (facteur prédisposant (e.g. sol sableux drainant), déclenchant (e.g. sécheresse) et aggravant (e.g. feu de forêt) ; Landmann, 1994; Manion, 1981; Nageleisen et al., 2010) mènent à la mort progressive des arbres, parfois sur de larges surfaces. Ces changements peuvent aussi aboutir à des processus de mortalité très rapides, suite à des pullulations d'insectes par exemple. Dans ce cadre, la gestion des peuplements en crise va devenir de plus en plus fréquente.

Les perturbations naturelles sont des moteurs majeurs de la dynamique des écosystèmes forestiers (Bengtsson et al., 2003; Kuuluvainen, 2016; Pickett and White, 1985). Tempêtes, incendies, sécheresses et pullulations d'insectes modulent fortement et durablement la structure et le fonctionnement des forêts (Pickett and White, 1985; Van Lierop et al., 2015). Elles conduisent à la création de nouvelles ressources et de nouveaux habitats portant des assemblages riches en espèces à haute valeur de conservation, par la transformation des éléments et des structures présents au sein de l'écosystème avant perturbation (Franklin et al., 2000; Swanson et al., 2011; Thorn et al., 2018a). Ainsi, les banques de graine deviennent régénération forestière et les arbres vivants deviennent bois mort (Swanson et al., 2011). Ils sont dénommés héritages biologiques matériels ("*biological legacies*" en anglais) et ont une grande importance dans les processus de résilience des forêts (Franklin et al., 2000; Johnstone et al., 2016; Swanson et al., 2011). Toutefois, ces perturbations peuvent s'opposer aux objectifs de production de bois en causant des baisses d'accroissements (e.g., les sécheresses ; Anderegg et al., 2015) et des dépréciations de la qualité marchande des arbres ; la perturbation entrant en compétition avec l'exploitation forestière pour la même ressource bois (Schmiegelow et al., 2006).

La question de la gestion des peuplements forestiers en crise et de la préparation aux changements actuels et futurs est centrale (Brunier et al., 2020; Gauquelin, 2010; Legay and Mortier, 2006). Au-

aujourd'hui, la méthode de gestion généralement mise en œuvre en réponse à un dépérissement est la coupe sanitaire de récupération. Elle est définie par l'exploitation en urgence des arbres dépérissants ou morts, pendant un phénomène de dépérissement, et hors du cadre de la gestion normalisée des peuplements forestiers (Gauquelin, 2010; Lindenmayer and Noss, 2006). Elle poursuit principalement deux objectifs : (i) la récupération d'une part significative de la valeur économique des produits accidentels ("*salvage logging*") ; (ii) l'évitement ou le freinage de l'épidémie dans le cas de pullulations d'insectes à potentiel ravageur ("*sanitation logging*") (Müller et al., 2019; Thorn et al., 2018a).

Il s'est constitué ces dernières années une base relativement riche d'études questionnant les effets de ces pratiques sur le fonctionnement des écosystèmes forestiers et des services écosystémiques rendus (Encart 1 ; Leverkus et al., 2020; Lindenmayer et al., 2008; Thorn et al., 2018a). À travers cette revue de littérature, nous restituons ici les principaux résultats et consensus issus de ces différentes études, dans l'objectif central d'améliorer si besoin les pratiques aujourd'hui mises en œuvre dans les peuplements gérés dépérissants. L'objectif est d'analyser la réponse de différents facteurs de fonctionnement de l'écosystème forestier à la pratique de la coupe sanitaire mise en œuvre suite à un dépérissement, en comparant les peuplements perturbés ayant subi une coupe sanitaire et les peuplements perturbés non exploités. Pour cela, nous avons sélectionné des services écosystémiques associés à la notion de résilience de l'écosystème forestier, c'est-à-dire "la capacité d'une forêt à absorber les perturbations et à se réorganiser en cas de changement afin de conserver un fonctionnement et une structure similaires" (Scheffer, 2009). Cette capacité de réorganisation est assurée par des facteurs biotiques, nous avons sélectionné la biodiversité ainsi que la capacité de maintien d'une végétation ligneuse ; et abiotiques, nous avons sélectionné la résistance à de futures perturbations, les caractéristique physico-chimiques du sol et la quantité de bois mort. Nous avons jugé ces différents facteurs comme faisant partie de la mémoire écologique participant à la résilience écologique (Bengtsson et al., 2003; Johnstone et al., 2016). En outre, Thorn et al. (2018a) annoncent que les espèces de milieux forestiers ouverts sont plutôt favorisées par les coupes sanitaires, aux dépens des espèces de milieux forestiers fermés. Nous avons souhaité vérifier ce résultats en associant certaines guildes écologiques aux milieux forestiers fermés et ouverts selon les préférences connues dans la littérature.

Encart 1: Exemple du parc national de la forêt de Bavières

Le parc national de la forêt de Bavière en Allemagne ("Bavarian National Park"), à la frontière avec la République Tchèque et l'Autriche, est connu pour l'étude des dépérissements et des coupes sanitaires (Thorn et al., 2017). Suite aux perturbations causées par différentes tempêtes depuis les années 1980, plusieurs larges épidémies de scolyte typographe (*Ips typographus*) se sont déclarées dans les peuplements dominés par l'Épicéa commun (*Picea abies*). Dans la zone cœur du parc, une stratégie de laisser-faire a été adoptée tandis que dans les zones périphériques gérées, les peuplements infestés ont été exploités. Avec un recul de près de dix ans, il apparaît que les coupes sanitaires ont induit une baisse du nombre d'espèces de champignons lignicoles et de coléoptères saproxyliques¹ et du nombre d'espèces de mousses et lichens épiphytes suite à la réduction de la quantité de bois mort et à la modification drastique du microclimat (Cours et al., 2021; Thorn et al., 2014, 2015, 2016a, 2017).



Figure 8.1 – À gauche : paysage forestier suite à une pullulation du coléoptère *Ips typographus* dans la zone cœur du parc de Bavière ; à droite : zone de régénération forestière naturelle abondante suite au dépérissement des épicéas. Photos : G. Parmain, projet CLIMTREE.

¹saproxylique : terme décrivant toute espèce qui dépend, pendant une partie de son cycle de vie, du bois mort en décomposition provenant d'arbres vivants, affaiblis ou morts ou d'espèces dépendant directement de ses ressources et habitats (e.g. prédateurs, parasitoïdes, etc.) (Bouget et al., 2019; Stokland et al., 2012)

²épiphyte : terme décrivant toute plante ou lichen qui croît sur un autre végétal. Le bois mort est un support important pour de nombreuses espèces de mousses en forêts tempérées (Gosselin et al., 2017a)

8.2 Matériels et méthodes

Nous définissons comme coupe sanitaire de récupération l'exploitation des arbres vivants dépérissants ainsi que celle des arbres récemment morts. Nous avons sélectionné les différents services écosystémiques à partir d'une précédente méta-analyse et ciblé ceux associés à une notion de résilience (Tab. 8.1; Leverkus et al., 2020; Scheffer, 2009). Nous avons ajouté le service de provision de biodiversité (non étudié par Leverkus et al., 2020) puisqu'elle a une importance avérée dans le fonctionnement et la résilience des écosystèmes, en participant directement à leur réorganisation suite à une perturbation (Bengtsson et al., 2003; Schulze, 2012). La biodiversité a été étudiée au travers des changements de richesse spécifique (i.e. le nombre d'espèces) et/ou de composition des assemblages d'espèces. De plus, nous avons étudié la résilience du peuplement forestier, à travers la reconstitution du recouvrement de la végétation ligneuse

forestière (i.e. le recouvrement, l'abondance et/ou la biomasse de semis ou de fourrés ; Tab. 8.1). Nous avons jugé que le maintien du recouvrement occupé par la régénération forestière après une perturbation, sans tenir compte de sa composition dendrologique, permet un retour plus rapide à la structure et au fonctionnement pré-perturbation. Nous avons relevé les effets des coupes sanitaires sur le stock de bois mort, l'un des principaux héritages biologiques après un dépérissement et participant de fait à la résilience de l'écosystème par le maintien des communautés forestières colonisant ce support (Bengtsson et al., 2003; Cours et al., 2021; Franklin et al., 2000; Swanson et al., 2011; Thorn et al., 2017). Par ailleurs, les perturbations interagissent dans le temps : une tempête peut faciliter la survenue d'une pullulation de ravageurs, une sécheresse la survenue d'un incendie de forêt (Seidl et al., 2017). Par conséquent, nous avons noté les effets potentiels des coupes sanitaires sur la survenue de perturbations ultérieures (i.e. facilitation, neutre ou inhibition). Enfin, de nombreux processus liés au sol sont importants pour un retour plus rapide à une structure et un fonctionnement de l'écosystème proche de l'état pré-perturbation : banque de graine, tassement ou cycle des nutriments (Albrich et al., 2020). Nous avons donc relevé les effets des coupes sanitaires sur divers caractères de régulation des caractéristiques physico-chimique du sol (Tab. 8.1 ; Pereg et al., 2018).

Table 8.1 – *Sommaire des différents services écosystémiques étudiés dans le cadre de cette revue de la littérature et le nombre de références associées (une même référence peut décrire la réponse de plusieurs services écosystémiques). Liste venant en partie des services étudiés par Leverkus et al. (2020).*

Groupe de services écosystémiques	Service écosystémique	Nombre de références
Biodiversité	Provision de biodiversité	89
Maintien du cycle de vie, habitat et protection du patrimoine génétique	Recouvrement par la végétation	62
	Quantité de bois mort	25
Régulation des événements extrêmes	Résistance à la perturbation suivante	20
	Tassement	4
Régulation des caractéristiques physico-chimique du sol	Stock de carbone	4
	Quantité de nutriments	10
	Capacité d'échange cationique	2

Par la suite, nous avons effectué en mars 2021 une recherche dans le Web of science (WOS) en utilisant la phrase de recherche "*salvage logging*" OR "*sanitation logging*" OR "*sanitary logging*" OR "*sanitation cutting*", qui nous a livré 527 articles scientifiques. Nous avons sélectionné les articles traitant des services écosystémiques identifiés (Tab. 8.1) ainsi que mettant en œuvre une comparaison claire entre peuplements perturbés non-exploités et peuplements perturbés exploités par coupe sanitaire de récupération (Leverkus et al., 2018b). Au final, nous avons étudié l'effet des coupes sanitaires à partir de 193 études publiées de 1996 à 2021 (Fig. 8.2) et procédé à un comptage de votes, en notant pour chaque étude le sens des effets significatifs de la coupe sanitaire en comparaison des zones perturbées par le même facteur mais non-exploitées. Pour tout effet significativement positif sur le service étudié un score de 1 a été attribué, pour tout effet significativement négatif, un score de -1, et un score de 0 a été attribué pour toute absence d'effet (i.e. absence de significativité de l'effet). Ainsi, nous avons pu mesurer l'effet moyen des coupes sanitaires sur la biodiversité et sur les différents services écosystémiques identifiés, par le log-ratio des fréquences d'effets positifs par la fréquence d'effets négatifs (Equation 8.1). La principale limite à notre travail et celle associée plus généralement à la méthode de la revue de la littérature, est que nous ne pouvons pas pondérer notre analyse par l'incertitude et la magnitude des effets des coupes sanitaires associés à chaque étude.

$$\text{Effet moyen des coupes sanitaires} = \log \left(\frac{\text{fréquence d'effets positifs} + 1}{\text{fréquence d'effets négatifs} + 1} \right) \quad (8.1)$$

Concernant la biodiversité, nous avons recensé les résultats selon les groupes taxonomiques et les guildes écologiques étudiés dans les différents articles. Par exemple, pour les oiseaux, nous avons noté les effets des coupes sanitaires sur l'ensemble du groupe et sur différentes guildes spécifiques (e.g. les oiseaux de milieux forestiers fermés ou ouverts) à partir des résultats directement fournis par les articles étudiés (Tab. 8.2). Nous avons aussi relevé le niveau d'intensité des coupes sanitaires comme variable quantitative continue, i.e. la quantité de bois mort ou dépérissant prélevée en proportion du stock initial, lorsque l'information était disponible et nous avons étudié son effet sur les réponses de la biodiversité. Par conséquent, nous n'avons pas utilisé les données brutes, pour les réanalyser dans le cadre d'une méta-analyse, mais seulement les résultats présentés dans le corps des articles.

Table 8.2 – *Liste des groupes taxonomiques dont les réponses ont été étudiées dans le cadre de la revue systématique de la littérature, l'habitat associé à dire d'expert (forestier ouvert ou fermé) ainsi que le nombre de références (une même référence peut décrire la réponse de plusieurs groupes ou guildes).*

Groupe taxonomique ou guildes écologique	Habitat associé	Nombre de références
Arthropodes		15
Coléoptères Carabidae	Forestier ouvert	3
Coléoptères saproxyliques	Forestier ouvert	7
Lépidoptères (papillons)	Forestier ouvert	1
Pollinisateurs	Forestier ouvert	3
Autres		3
Champignons		5
Saproxyliques	Forestier fermé	3
Autres		2
Lichens		2
Epixyliques (sur l'écorce)		2
Mammifères		8
Chauves-souris		2
Rongeurs		2
Autres		5
Oiseaux		31
Cavicoles	Forestier fermé	8
Nicheurs en buisson	Forestier ouvert	2
Nicheurs en canopée	Forestier fermé	2
Nicheurs au sol	Forestier ouvert	2
Spécialistes des milieux fermés	Forestier fermé	4
Spécialistes des milieux ouverts	Forestier ouvert	4
Autres		9
Plantes		33
Bryophytes (mousses)		7
Début de succession	Forestier ouvert	3
Fin de succession	Forestier fermé	7
Vasculaires		9
Autres		13

Par la suite, nous n'avons conservé pour l'analyse que les groupes taxonomiques de niveau inférieur ou supérieur dans la typologie, pour lesquels nous avons jugé avoir un nombre assez élevé d'études (au moins quatre) pour apporter des résultats à discuter.

Dans l'objectif de vérification du résultat annoncé par Thorn et al. (2018a) dans le cadre de notre synthèse, i.e. les coupes sanitaires favorisent les espèces de milieux forestiers ouverts aux dépens des espèces de milieux forestiers fermés ; nous avons inféré une préférence d'habitat pour certains groupes taxonomiques à partir des connaissances disponibles dans la littérature à leur sujet (Tab. 8.2). Il est par exemple connu que la diversité du groupe des coléoptères saproxyliques répond favorablement à l'ouverture de la canopée (Tab. 8.2 ; Bouget et al., 2014a; Seibold et al., 2016). De même, concernant la régénération forestière, nous avons caractérisé certains traits fonctionnels réagissant aux coupes sanitaires

d'après la littérature. Nous avons ainsi renseigné, dans la limite des connaissances disponibles, la tolérance à l'ombrage en trois catégories, i.e. intolérance (e.g. pin d'Alep (*Pinus halepensis*)), tolérance intermédiaire (e.g. épicéa commun), tolérance forte (e.g. épinette noire (*Picea mariana*)), et la capacité à rejeter de souche à l'aide de différentes sources (Burns and Honkala, 1990; Martin and Gower, 1996; Rameau et al., 1989).

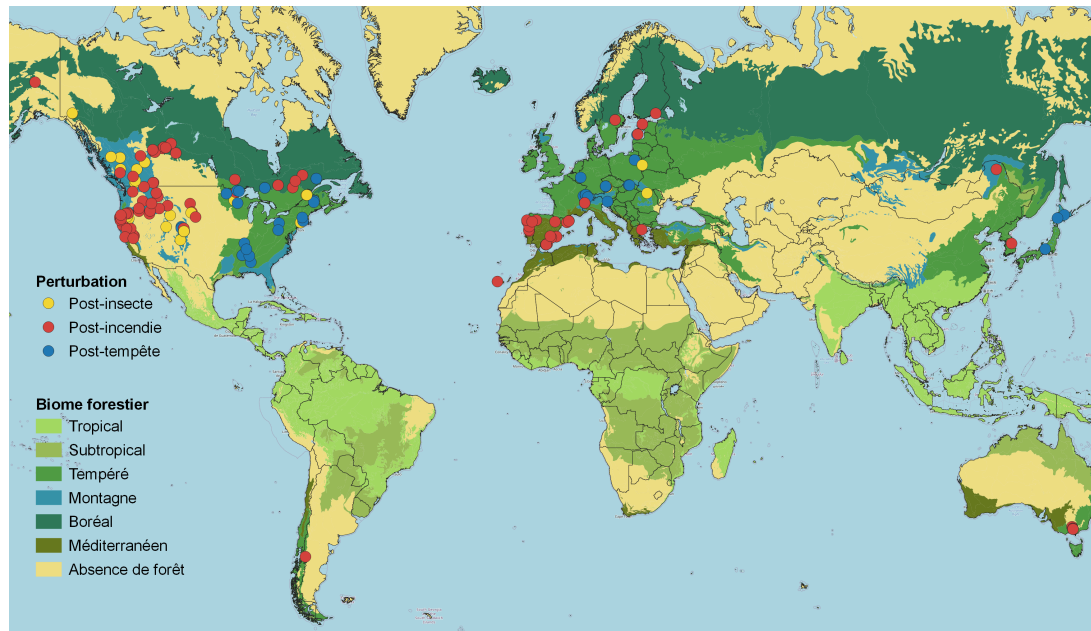


Figure 8.2 – Localisation des études recensées dans le cadre de ce travail. Les études concernant les coupes sanitaires étudient majoritairement les effets consécutifs aux incendies de forêt (en rouge), tempêtes (en bleu) et pullulations d'insectes à potentiel ravageur (jaune).

8.3 Résultats

Dans un premier temps, notre synthèse de la littérature montre que les effets des coupes sanitaires sur les communautés forestières ont été principalement étudiés sur les plantes, les oiseaux ainsi que les arthropodes, largement dominés par la réponse des insectes (Tab. 8.2). Par ailleurs, les effets des coupes sanitaires après incendie (111 études), tempête (50 études) ou épidémie de ravageur (32 études) sont plus largement étudiés que pour d'autres facteurs de perturbation (e.g. les sécheresses, les vagues de chaleurs, etc. ; Fig. 8.2). Enfin, nous remarquons que les études sont majoritairement concentrées en Amérique du Nord et en Europe, au sein des biomes de forêt de montagne (72 études), tempérée (65 études), boréale (26 études) et méditerranéenne (30 études ; Fig. 8.2). Par ailleurs, certaines perturbations sont associées à des zones géographiques spécifiques, i.e. feux de forêt au sein des forêts méditerranéennes et boréales, et côte ouest de l'Amérique du Nord ; tempêtes concernant le domaine atlantique et les côtes japonaises (Fig. 8.2).

8.3.1 Effets sur la biodiversité

En moyenne, l'abondance et la richesse spécifique des arthropodes (15 études), des oiseaux (31 études) et des plantes (33 études) répondent négativement aux coupes sanitaires (Fig. 8.3A). De même, l'abondance des mammifères (8 études) est négativement affectée par les coupes sanitaires (pas d'études concernant la richesse spécifique ; Fig. 8.3A). Parmi les arthropodes, les coléoptères saproxyliques répondent négativement aux coupes sanitaires (Fig. 8.3B). Les oiseaux cavicoles (i.e. nichant dans les

cavités d'arbres) sont également négativement affectés par les coupes sanitaires, de même que les espèces dites dans les études, spécialistes des milieux forestiers fermés (4 études ; Fig. 8.3B). Au contraire, les oiseaux dits spécialistes des milieux forestiers ouverts dans les études, répondent positivement aux coupes sanitaires (4 études ; Fig. 8.3B). Les bryophytes sont négativement affectées par les coupes sanitaires, tandis que les plantes vasculaires ont des réponses relativement neutres aux coupes sanitaires, potentiellement positives en abondance (Fig. 8.3B).

Le niveau d'intensité de la coupe sanitaire a peu d'effet sur les réponses aux coupes sanitaires en proportion de la biodiversité, (Fig. 8.4). À des niveaux d'intensité de prélèvement inférieurs à 50%, les réponses de la biodiversité restent encore relativement négatives (Fig. 8.4). La plupart des études étudient des coupes sanitaires dont l'intensité est égale ou supérieure à 75% (Fig. 8.4).

Enfin, les groupes taxonomiques associés aux milieux forestiers fermés répondent négativement aux coupes sanitaires (Fig. 8.5). En revanche, les groupes taxonomiques associés aux milieux forestiers ouverts sont favorisés par les coupes sanitaires, surtout en abondance (Fig. 8.5).

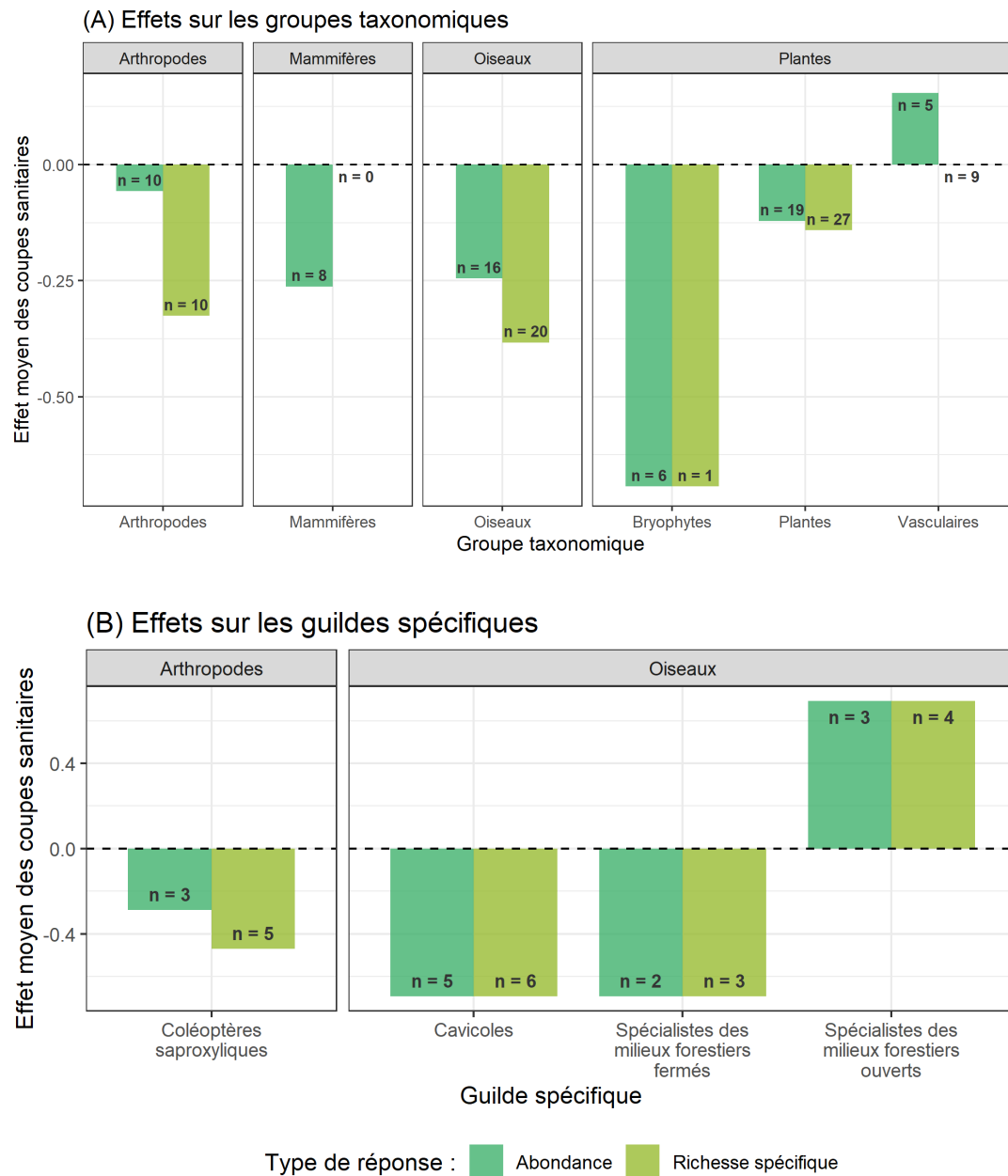


Figure 8.3 – Effets des coupes sanitaires (A) sur les groupes taxonomiques étudiés et (B) sur des guildes spécifiques de biodiversité (en abondance et en richesse spécifique).

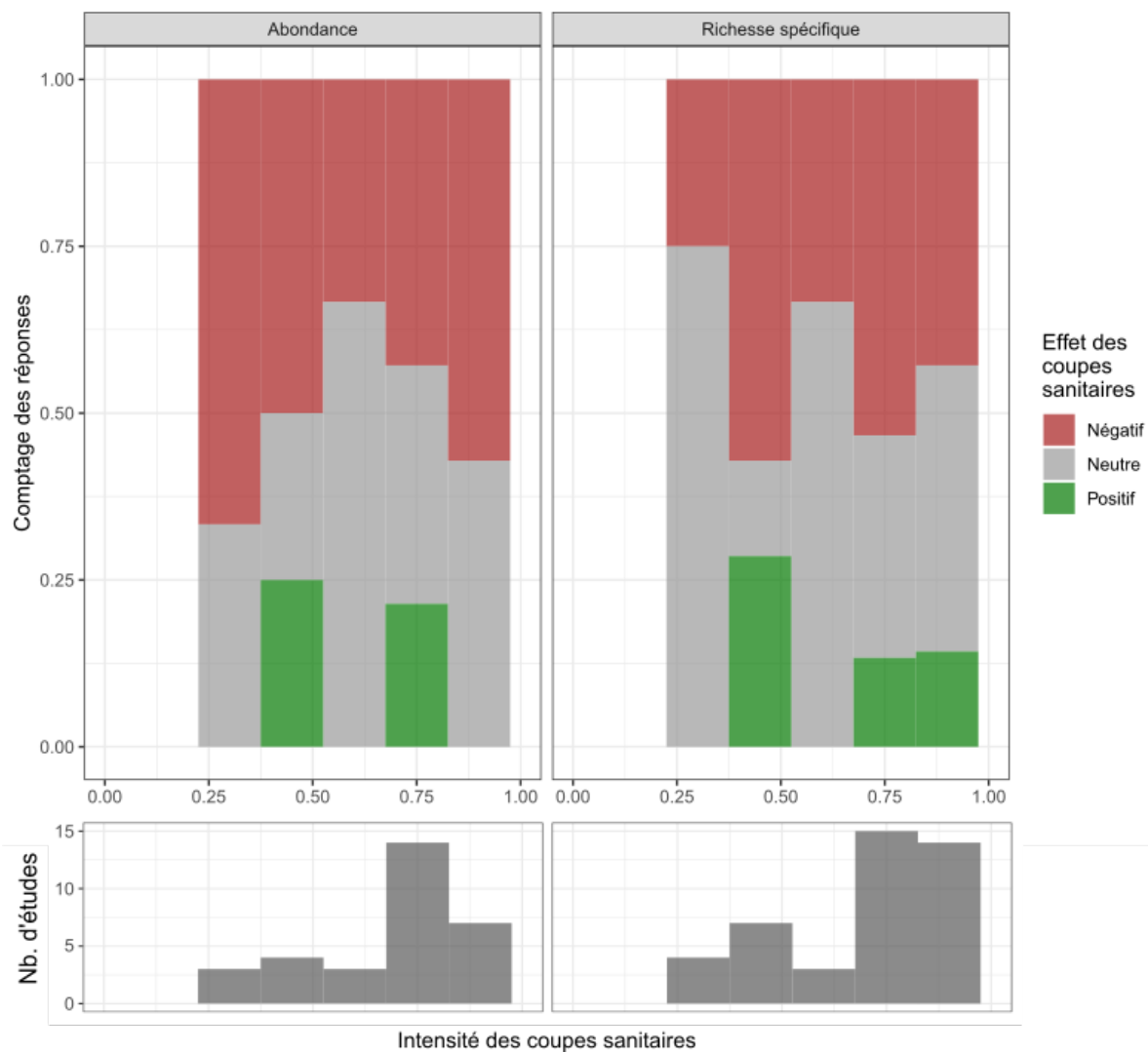


Figure 8.4 – Réponse de l'ensemble des réponses de la biodiversité en abondance et en richesse spécifique selon l'intensité des coupes sanitaires. On remarque que la plupart des études montrent une intensité des coupes sanitaires de 75% ou plus (histogrammes du bas). En proportion, les effets négatifs restent importants même à de faibles intensités (e.g. < 50%).

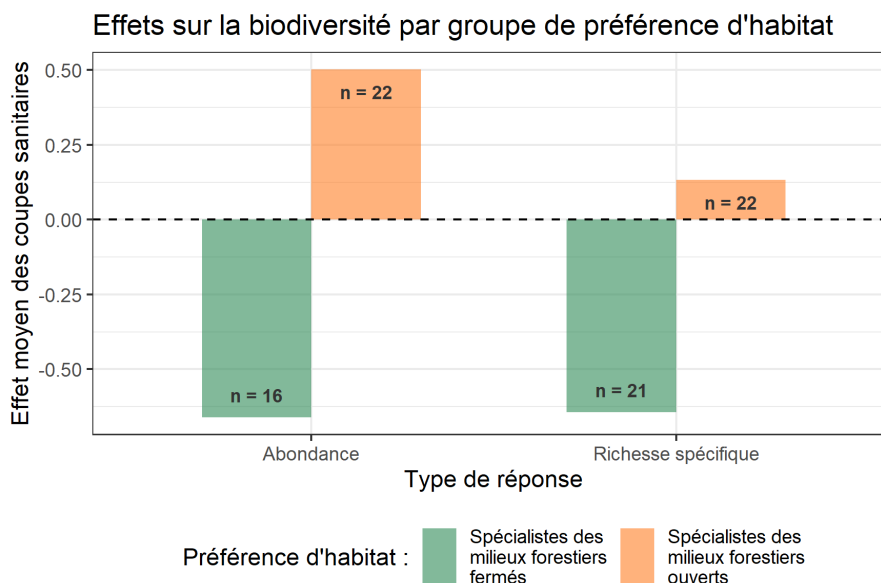


Figure 8.5 – *Effet moyen des coupes sanitaires sur l'abondance et la richesse spécifiques des espèces jugées liées aux habitats forestiers fermés (vert) et ouverts (orange). "n" est le nombre d'études concernant chaque groupe et chaque métrique.*

8.3.2 Effets sur les services écosystémiques

Les coupes sanitaires ont pour conséquence directe la forte réduction de la quantité de bois mort (Fig. 8.6). Par ailleurs, elles semblent affecter les perturbations naturelles ultérieures : elles diminuent le risque de pullulations postérieures de ravageurs mais augmentent le risque d'incendie (Fig. 8.6). En outre, nous remarquons des effets négatifs des coupes sanitaires sur le succès global de la régénération forestière (Fig. 8.6). Néanmoins, ce résultat est contrasté selon le groupe d'essences considéré, la capacité des essences à rejeter de souche ou encore leur degré de tolérance au couvert (Fig. 8.7). Ainsi, l'effet négatif des coupes sanitaires sur la régénération est surtout effectif pour les essences ne se régénérant que par graines, et donc principalement les espèces de conifères (Fig. 8.7). Au contraire, les essences ayant pour capacité de rejeter de souche, principalement les essences feuillues, ne sont pas affectées par les coupes sanitaires (Fig. 8.7). Enfin, les études mettent en avant des conséquences généralement négatives des coupes sanitaires sur les caractéristiques physico-chimiques du sol (Fig. 8.6). En effet, les coupes sanitaires se traduisent par un moindre stock de carbone dans le sol (4 études), une moindre capacité d'échange cationique (2 études), un plus fort tassement du sol (4 études) et surtout, une plus faible quantité de nutriments (10 études ; Fig. 8.6).

8.4 Discussion

8.4.1 Contextes d'étude des conséquences écologiques des coupes sanitaires

Les études des conséquences écologiques des coupes sanitaires se concentrent autour de trois types de perturbations : les tempêtes, les incendies et les pullulations de ravageurs. Nous n'avons pas trouvé mention d'étude des coupes sanitaire suite à d'autres facteurs de perturbation émergents tels que les sécheresses (hormis notre étude pyrénéenne ; Cours et al., 2021). Il est probable que les sécheresses ou les vagues de chaleur soient des facteurs déclenchants ou prédisposants des dépérissements en association au facteur identifié (e.g. sécheresse avant épidémie de ravageur ou incendie de forêt ; Rouault et al., 2006; Sallé et al., 2014; Seidl et al., 2017). Par ailleurs, sécheresses et vagues de chaleurs apparaissent

associées au changement climatique et les dépérissements liés à ces facteurs sont des phénomènes en émergence (Senf and Seidl, 2021b; Senf et al., 2020).

8.4.2 Des effets généralement négatifs sur la biodiversité mais différents selon l'habitat de prédilection de la guildes écologique

La synthèse des études montre des réponses généralement négatives aux coupes sanitaires de la part des différents groupes taxonomiques étudiés (Fig. 8.3A). Notre observation rejoint les résultats d'une méta-analyse récente réalisée par Thorn et al. (2018a). Les coupes sanitaires visent à extraire des arbres dépérissants et morts et affectent par conséquent la quantité de ressources saproxyliques et l'hétérogénéité interne des peuplements et participent à l'ouverture du milieu (Cours et al., 2021). Le bois mort constitue un des principaux héritages biologiques matériels présents suite à une perturbation naturelle et contribuant à la résilience du milieu forestier (Cours et al., 2021; Swanson et al., 2011; Thorn et al., 2018a; Waldron et al., 2013). Les arbres morts ou dépérissants générés par la perturbation fournissent habitat et ressource trophique pour les espèces saproxyliques (Encart 1), notamment cavicoles : la création de loges y est facilitée et le bois est colonisé par une grande abondance d'arthropodes facilitant l'alimentation des insectivores (Drever et al., 2009; Murphy and Lehnhausen, 1998; Ojeda et al., 2007). De plus, un écosystème forestier perturbé et non exploité présente une grande hétérogénéité structurale qui favorise la présence d'un grand nombre d'espèces et d'une grande abondance d'individus (Fig. 8.3 ; Thorn et al., 2017).

En accord avec les résultats de Thorn et al. (2018a), la réponse des groupes taxonomiques est différente selon l'habitat préférentiellement recherché (Figs. 8.3B and 8.5). Les groupes préférant les habitats forestiers fermés répondent négativement aux coupes sanitaires (Fig. 8.5). C'est le cas notamment chez les oiseaux (Fig. 8.3A ; voir par exemple Castro et al., 2010) : les coupes sanitaires ont tendance à réduire l'abondance et la richesse spécifique des oiseaux cavicoles autant primaires (e.g., les pics) que secondaires (e.g., les mésanges ou les sittelles ; Hutto and Gallo, 2006; Morissette et al., 2002). Ce groupe des oiseaux cavicoles concentre environ 40% de l'avifaune forestière en France et de fait, est très important, autant numériquement que fonctionnellement dans les écosystèmes forestiers (Blondel, 2005). Au contraire, les groupes préférant les milieux forestiers ouverts répondent généralement positivement aux coupes sanitaires, exception faite du groupe des coléoptères saproxyliques, pénalisés par les prélèvements de substrats (Fig. 8.3B and 8.5). Par exemple, en Espagne, Rost et al. (2012) montrent que des espèces d'oiseaux associées à des milieux plus ouverts sont favorisées par l'extraction des chandelles post-incendie ; des espèces telles que le moineau domestique (*Passer domesticus*) ou encore l'alouette lulu (*Lullula arborea*). D'ailleurs, dans les régions où les oiseaux liés à des milieux ouverts sont en danger et voient leur population décliner au cours du temps (voir par exemple le Suivi temporel des oiseaux communs (STOC) ; Fontaine et al., 2020), Rost et al. (2012) identifient les zones de coupes sanitaires comme pouvant représenter des zones refuges. Dans le parc national de la forêt de Bavière, Thorn et al. (2016d) montrent que les zones perturbées par une tempête puis suivies d'une coupe sanitaire, sont caractérisées par la présence de deux espèces de pipit : le pipit des arbres (*Anthus trivialis*) et le pipit spioncelle (*Anthus spinoletta*), deux espèces connues pour se nourrir au sein de milieux assez ouverts.

Par conséquent, il résulte généralement des coupes sanitaires une altération des communautés forestières pouvant affecter la capacité de résilience de l'écosystème. Les coupes sanitaires induisent un changement des communautés dont la composition s'éloigne des assemblages forestiers préexistant au dépérissement, par un effet additif au dépérissement (Castro et al., 2010; Cours et al., 2021; Lindenmayer et al., 2018; Michalová et al., 2017; Morissette et al., 2002).

Cette altération des communautés peut perdurer longtemps après la coupe sanitaire. Par exemple, 20 ans après les coupes sanitaires ayant suivi une épidémie de tordeuse du bourgeon (*Choristoneura*

fumiferana) dans des peuplements de sapin baumier (*Abies balsamea*) au Canada, le changement dans l'assemblage des coléoptères saproxyliques était encore perceptible (Norvez et al., 2013). Cependant, les effets à long terme sur la biodiversité restent à approfondir, tant on manque d'études sur la dynamique des communautés à long cours, i.e. plus de 5 ans après perturbation/exploitation (Thorn et al., 2018a).

En gestion forestière, les coupes d'exploitation sont des perturbations, mais la matière ligneuse issue des mortalités d'arbres est exportée. Les coupes sanitaires s'apparentent pour l'écosystème forestier à des perturbations s'additionnant en sévérité à la perturbation initiale et ramenant alors l'écosystème vers des stades plus précoces d'évolution (Castro et al., 2010; Cours et al., 2021; Leverkus et al., 2014; Michalová et al., 2017; Morissette et al., 2002; Orczewska et al., 2019; Rumbaitis del Rio, 2006). En revanche, les coupes sanitaires agissent comme force négative en soustrayant les héritages biologiques produits par la perturbation naturelle, là où cette dernière agit en transformant les substrats et habitats et hétérogénéise la structure forestière (Bengtsson et al., 2003; Franklin et al., 2000; Johnstone et al., 2016; Swanson et al., 2011). Une originalité de notre revue de littérature est la prise en compte de l'intensité de la coupe sanitaire : il apparaît que les réponses de la biodiversité sont globalement négatives, même à des niveaux relativement faibles d'intensité de prélèvement (Fig. 8.4). La colonisation d'un habitat par une espèce ou sa disparition ne sont pas liées par une fonction linéaire avec la quantité de cette habitat. Müller et Bütler (2010) ont montré que pour le bois mort, la colonisation du substrat est associée à un effet seuil : il est nécessaire d'avoir une certaine quantité de bois mort pour voir rapidement se développer un grand nombre d'organismes saproxyliques (30 à 50 m³.ha⁻¹ dans les forêts feuillues de plaine). Cependant, en dessous de cette valeur "seuil" la colonisation du substrat bois mort se fait par un faible nombre d'espèces. Ainsi, même si la coupe sanitaire prélève une quantité relativement faible (e.g. 50%) de bois mort et déperissant, si la quantité restante est inférieure à la valeur du seuil, alors les organismes associées au bois mort ne pourront pas efficacement coloniser le substrat restant.

Les coupes sanitaires semblent affecter l'élasticité des écosystèmes forestiers en contribuant à rallonger le temps de résilience (i.e. "perte d'élasticité"). Elles affectent généralement négativement les espèces associées aux milieux forestiers fermés (i.e. de fin de succession), au profit des espèces de milieux forestiers plus ouverts (i.e. de début de succession ; Fig. 8.5). En comparaison, dans les milieux perturbés non exploités, l'hétérogénéité à échelle fine garantit une superposition dans l'espace et dans le temps d'espèces liées à des milieux fermés et non fermés (Hanson and Stuart, 2005; Larrieu et al., 2014; Rumbaitis del Rio, 2006). Les coupes sanitaires ramènent donc généralement les écosystèmes vers des stades plus précoces de succession, pouvant, dans un contexte de changement rapide des conditions environnementales, entraver la résilience de l'écosystème forestier en imposant un temps de retour plus long à un état post-perturbation proche de l'état initial (Leverkus et al., 2014; Lindenmayer et al., 2008; Michalová et al., 2017).

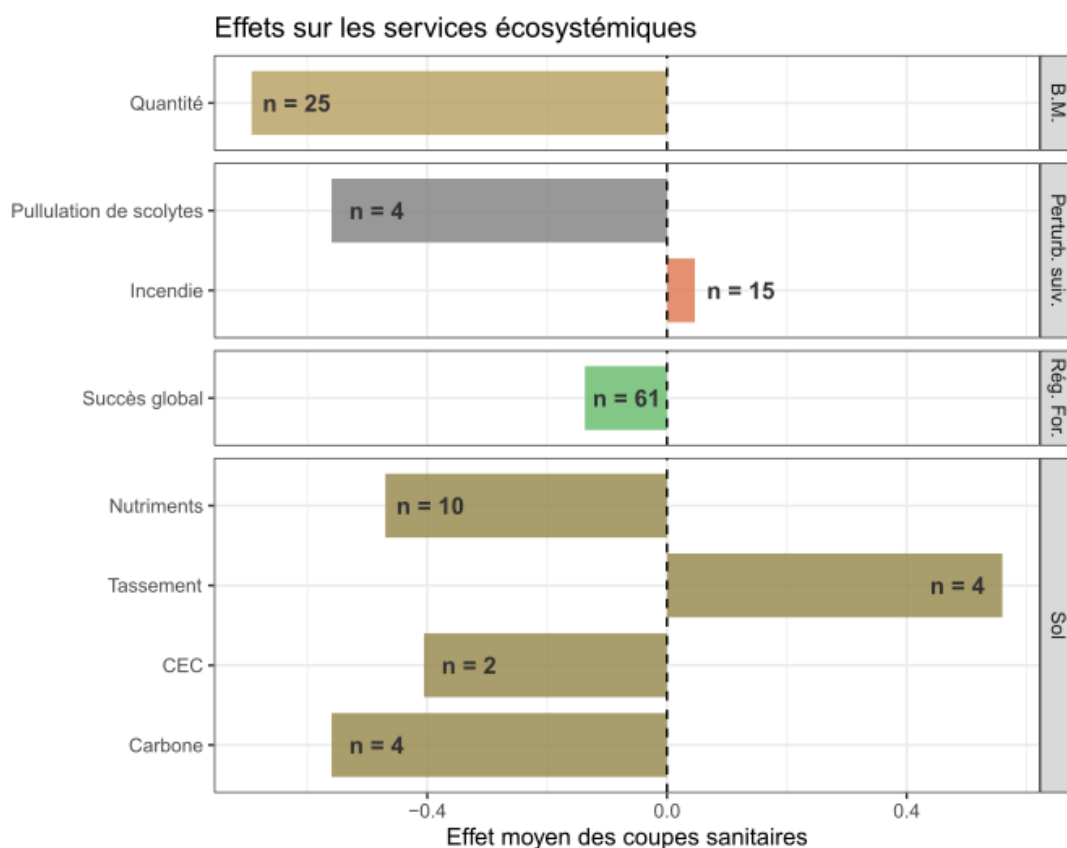


Figure 8.6 – Effets des coupes sanitaires sur les services écosystémiques. "B.M." = bois mort ; "Perturb. suiv." = perturbation suivante ; "Rég. For." = régénération forestière ; "CEC" = capacité d'échange cationique.

8.4.3 Des sols généralement dégradés

En général, les coupes sanitaires dégradent les caractéristiques physico-chimiques des sols (Fig. 8.6). Néanmoins, la majorité des travaux étudient les effets des coupes sanitaires sur les sols suite à un incendie (86%). Nos résultats concernent donc principalement les conséquences des coupes sanitaires suite à cette perturbation. Suite à une coupe sanitaire, les sols apparaissent plus compacts (tassement suite au passage d'engins ; [García-Orenes et al., 2017](#); [Rab, 2004](#)), ont une capacité d'échange cationique réduite et contiennent une moindre quantité de carbone et de nutriments que les sols de peuplements perturbés mais non-exploités (Fig. 8.6 ; [García-Orenes et al., 2017](#); [Pereg et al., 2018](#)). Cette dégradation, principalement étudiée moins de cinq années après la coupe sanitaire, semble se maintenir dans le temps : après 10 à 11 ans, les sols des peuplements exploités après un incendie contiennent toujours significativement moins de carbone et d'azote et ont une capacité d'échange cationique réduite par rapport aux sols des peuplements incendiés et non exploités, traduisant une moindre quantité et qualité des matières organiques incorporées dans les sols ([Kishchuk et al., 2015](#)).

La réduction de la quantité de nutriments semble principalement être la conséquence de deux phénomènes. À court terme, il est observé une plus forte érosion des horizons de surface dans les peuplements perturbés et exploités que dans ceux non exploités ([García-Orenes et al., 2017](#); [Wagenbrenner et al., 2015](#)). Cette érosion entraîne une perte de matière organique servant de réservoir de nutriments à court terme, notamment l'azote et le phosphore. À long terme, le bois carbonisé contenant deux à neuf

fois plus d'éléments minéraux que le sol alentour, leur récolte peut induire une réduction à long terme de la quantité de nutriments dans le sol (Kishchuk et al., 2015; Marañón-Jiménez et al., 2013).

8.4.4 Des effets globaux relativement négatifs mais essence-dépendants sur la régénération naturelle

Nous n'observons qu'un faible effet négatif des coupes sanitaires sur la régénération naturelle, au vu du ratio d'études montrant des réponses positives et négatives (Fig. 8.6). Ce résultat négatif pourrait être le résultat de la dégradation des caractéristiques physico-chimiques des sols suite à la coupe sanitaire (voir 8.4). Une méta-analyse a montré que les coupes sanitaires n'ont pas d'effet significatif sur la régénération forestière (Leverkus et al., 2021b). Cependant, la réponse de la régénération forestière diffère selon les traits de vie des essences (Leverkus et al., 2021b). Ainsi, les espèces ayant la possibilité de se régénérer par la souche (i.e. presque uniquement les espèces feuillues) ne semblent pas défavorisées par les coupes sanitaires (Leverkus et al., 2014). Au contraire, les espèces ne se régénérant qu'à partir de graines sont négativement affectées (donc une majorité des espèces de conifères, mais aussi feuillues lorsque qu'elles ne sont pas présentes dans le peuplement pré-perturbation ; Fig. 8.7). Cette réponse négative des espèces ne se régénérant que par la production de graines est potentiellement le fait de deux processus. Premièrement, la soustraction des héritages biologiques (exportation des bois morts, arasement des galettes de chablis) ainsi que le tassement du sol par le passage des engins de débardage, peuvent entraîner une baisse de la capacité de germination de la banque de graines présente dans le sol au moment de la perturbation naturelle. Par exemple, la banque de graines du sol d'épicéa commun ou encore de pin sylvestre (*Pinus sylvestris*) germe préférentiellement sur les substrats bois mort ou à l'abri des bois au sol (Jonášová and Prach, 2004; Marzano et al., 2013; Svoboda et al., 2010). De même, les creux créés par les galettes de chablis suite aux tempêtes sont autant de milieux dans lesquels peuvent se développer les semis, surtout dans le cas d'humus de formes Mor ou Dysmoder induisant des litières épaisses (Kuuluvainen and Kalmari, 2003). Deuxièmement, la coupe sanitaire peut aboutir à une baisse de la capacité du milieu à être colonisé par de nouvelles graines. Par exemple, suite à un incendie, le geai des chênes, espèce forestière qui joue un rôle crucial dans la dissémination des chênes (*Garrulus glandarius*) (Ducouso and Petit, 1994), continue d'occuper les zones de chandelles brûlées et à enfouir dans le sol des glands de chêne (*Quercus* spp., dans l'étude, le chêne vert (*Q. ilex*)), facilitant ainsi le retour plus rapide à l'écosystème pré-perturbation. Au contraire, il a tendance à éviter les zones exploitées par des coupes sanitaires, retardant par conséquent la colonisation naturelle des chênes (Castro et al., 2012). Quatre années après la coupe sanitaire, il en résulte près de trois fois plus de semis de chêne dans les peuplements sans-intervention (Castro et al., 2012; Leverkus and Castro, 2017).

En addition du prélèvement du bois mort, l'une des modifications majeure des coupes sanitaires est l'ouverture de la canopée, affectant les conditions microclimatique et modulant fortement les communautés végétales et animales (Cours et al., 2021; Thorn et al., 2017). Par conséquent, les coupes sanitaires semblent négativement affecter les espèces sciaphiles et de demi-ombre sans affecter les espèces héliophiles (Fig. 8.7). Par exemple, dans une forêt de l'Etat du Minnesota (Etats-Unis), Palik et Kastendick (2009) ont montré que 12 années après une tempête et une coupe sanitaire, la composition de la régénération était encore différente entre les parcelles perturbées avec ou sans coupe sanitaire. Les surfaces non-exploitées étaient caractérisées par une plus grande abondance d'essences sciaphiles (Palik and Kastendick, 2009). En Slovaquie, suite à une pullulation de scolyte au sein de peuplements d'épicéa, Jonášová et Prach (2004) ont observé une augmentation de la densité d'espèces pionnières suite à la coupe sanitaire. Cependant, relativement peu de travaux étudient les effets des coupes sanitaires sur les espèces sciaphiles ou de demi-ombre, atténuant la robustesse de nos résultats (Fig. 8.7).

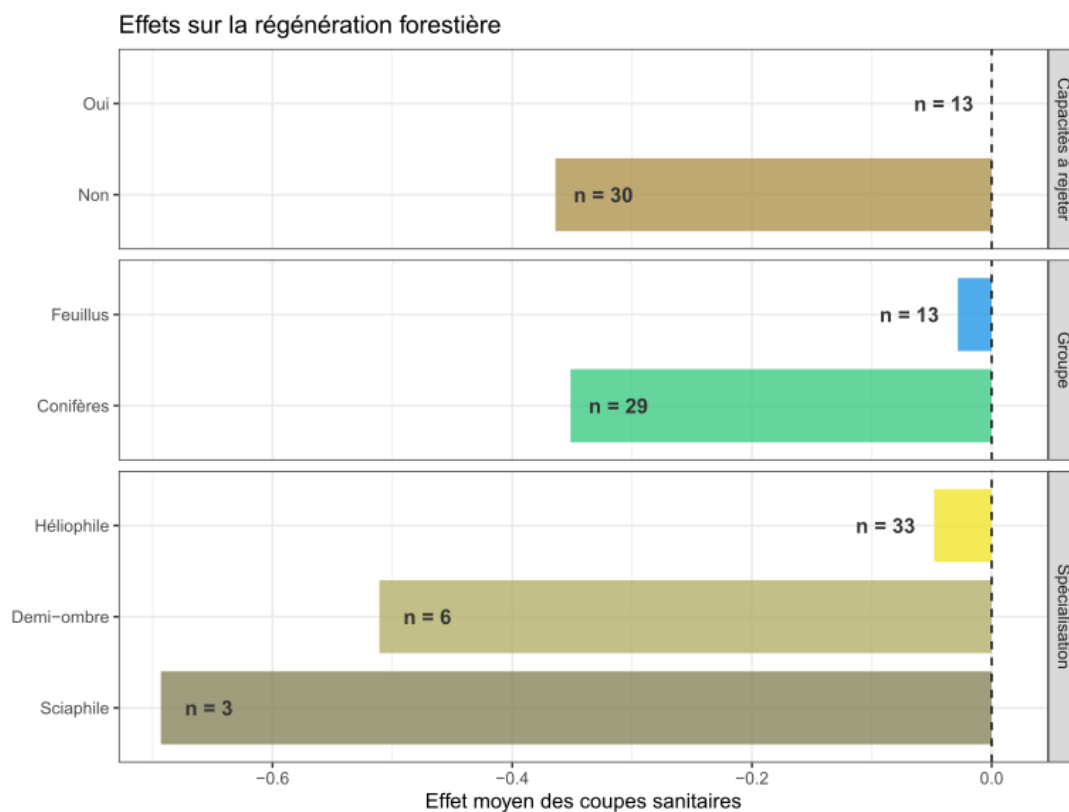


Figure 8.7 – Effets moyens des coupes sanitaires sur différentes caractéristiques de la régénération forestière. "n" est le nombre d'études traitant de l'élément considéré.

Par conséquent, bien que les coupes sanitaires semblent avoir des effets relativement faibles sur le succès global de la régénération forestière (Fig. 8.6), elles ont en réalité des répercussions sur son évolution (Fig. 8.7). Les études observent ainsi certaines capacités de remplacement d'espèces désavantagées par les coupes sanitaires (associés à certains héritages biologiques), par des espèces au contraire avantagées, et a priori associées à des stades de succession plus précoces (Fidej et al., 2016; Hanson and Stuart, 2005; Jonášová and Prach, 2004; Leverkus et al., 2014; Michalová et al., 2017; Orczewska et al., 2019; Palik and Kastendick, 2009; Taeroe et al., 2019). Par exemple, en Slovaquie, suite à une pullulation de scolytes dans des peuplements d'épicéas communs, Michalová et al. (2017) montrent que les parcelles exploitées après perturbation, contiennent moins d'espèces ligneuses de fin de succession, au profit d'espèces herbacées pionnières. D'ailleurs, dans le cas où l'essence se régénérant en masse suite à une perturbation n'est plus jugée adaptée au milieu dans le contexte d'augmentation des températures (e.g. anciennes plantations d'épicéas en plaine), il serait à étudier dans quelles conditions techniques une coupe sanitaire pourrait permettre une meilleure colonisation du milieu par de nouvelles espèces pionnières tout en ne remettant pas en cause le maintien du microclimat forestier et sa biodiversité.

Cependant, ces résultats sont majoritairement issus d'études à court terme (56% des études étudient l'effet des coupes sanitaires moins de cinq années après leur mise en œuvre). À plus long terme, les résultats semblent plus contrastés. Dans quatre cas d'étude, cette altération initiale de la composition de la régénération forestière perdure dans le temps, plus de 10 ans encore après la coupe sanitaire (Chen et al., 2014; Hanson and Stuart, 2005; Jonášová and Prach, 2004; Morimoto et al., 2019). Au Japon, dans un contexte post-tempête, Morimoto et al. (2019) montrent que ces modifications de composition sont encore observable 60 ans après les coupes sanitaires. Cependant, en parallèle, dans d'autres cas d'étude, les effets observés à court terme semblent s'être effacés au cours du temps entre les peuplements perturbés avec

et sans coupe sanitaire (Bādgers et al., 2020; Kurulok and Macdonald, 2007; Lang et al., 2009; Leverkus et al., 2021b). De fait, les effets à moyen et long terme (supérieurs à 10 ans) des coupes sanitaires sur la composition de la régénération, restent peu connus et doivent être mieux pris en compte dans de futures études. Par ailleurs, la plupart des études n'impliquent pas les pratiques associées aux coupes sanitaires. Pourtant, les choix de gestion appliqués suite aux coupes sanitaires ont d'importantes conséquences sur la résilience de l'écosystème. Par exemple, des plantations mono-spécifiques en plein, suite à des coupes rases sanitaires, diminuent la résilience de l'écosystème aux futures perturbations (Dhar et al., 2016; Levine et al., 2022; Thompson et al., 2007). Par exemple, Moreira et al. (2013) ont montré que les coupes sanitaires suivies d'un labour du sol limitaient le rétablissement des espèces indigènes tout en favorisant l'établissement d'espèces exotiques envahissantes. Il apparaît donc capital d'étudier à l'avenir, non pas simplement l'effet des coupes sanitaires sur la régénération, mais aussi l'effet de la gestion des jeunes peuplements.

8.4.5 Effets sur les perturbations suivantes : augmentation du risque d'incendie et réduction des futures pullulations d'insectes

Nos résultats indiquent une augmentation du risque d'incendie par les coupes sanitaires (Fig. 8.6). Cependant, les coupes sanitaires induisent en réalité deux effets antagonistes se neutralisant au bilan global : une augmentation du risque à court terme par la densité accrue des petits combustibles au sol (e.g. branches, écorces) produits par les opérations de coupe sanitaire mais une réduction à plus long terme par la récolte des gros combustibles (e.g. troncs) (Collins et al., 2012; Donato et al., 2013; Griffin et al., 2013; Leverkus et al., 2020, 2021a). Cependant, l'effet d'augmentation du risque incendie à court terme peut être limité en allongeant la période entre la perturbation et la coupe sanitaire. Si l'on maintient une période de cinq années environ entre la perturbation naturelle et la coupe sanitaire, il en résulte un risque d'incendie proche de zéro (Leverkus et al., 2020). Néanmoins, dans une recherche de compromis, cette période d'attente est incompatible avec les coupes sanitaires de sauvetage qui visent la récupération "urgente" des produits accidentels avant leur dépréciation ou la propagation d'insectes à potentiel ravageur (Leverkus et al., 2020). Par exemple, il est recommandé que les coupes sanitaires soient conduites dans les deux années suivant une tempête ou une sécheresse sévère pour réduire le risque de prolifération du typographe (Økland et al., 2016). Par ailleurs, le risque d'incendie à la suite d'une première perturbation naturelle et d'une coupe sanitaire, est lié aux choix de gestion postérieurs. Thompson et al. (2007) ont ainsi montré que les parcelles replantées avec des essences de conifères après un premier incendie, brûlaient avec plus de sévérité 15 ans après, en comparaison des parcelles brûlées mais non replantées.

A l'inverse, les coupes sanitaires semblent réduire le risque de futures pullulations de ravageurs (Fig. 8.6). Une étude conduite sur neuf années sur l'ensemble du territoire helvète conclut à l'efficacité des coupes sanitaires pour réduire les infestations de typographe (Stadelmann et al., 2013). Néanmoins, nous remarquons que cette conclusion, utilisée aujourd'hui pour proposer des politiques forestières à l'échelle internationale, se base finalement sur un nombre d'études relativement restreint ($n = 4$, Fig. 8.6 ; Leverkus et al., 2021a). Par conséquent, il apparaît urgent de mieux étudier les effets des coupes sanitaires sur la dynamique des populations de ravageurs forestiers opportunistes. En outre, toujours dans le cadre du typographe, des simulations montrent que les coupes doivent récolter la totalité des arbres morts ou affaiblis en début d'épidémie : une récolte inférieure à 95% des arbres pourrait ne pas avoir d'effet sur la dynamique de population du typographe, qui ne requiert qu'une faible quantité de ressources pour passer d'un statut endémique à épidémique (Dobor et al., 2020a,b; Kausrud et al., 2012; Leverkus et al., 2021a). Cette récolte, en plus d'être difficile dans les faits (Dobor et al., 2020b) exclut tout compromis avec les objectifs de conservation des communautés du bois mort (Thorn et al., 2018a, 2020). En revanche, Thorn et al. (2016b) ont montré que l'écorçage partiel des chablis formés suite à une tempête puis abandonnés sur le sol permettrait de trouver un compromis entre le contrôle des populations de scolytes typographes et le respect des objectifs de conservation de la biodiversité saproxylique, mais pas vis-à-vis de l'objectif économique (Hagge et al., 2019). Par ailleurs, Dobor et al. (2020b) ont montré

par simulation, que le maintien de forêts perturbées sans coupes sanitaires dans le paysage ne devrait pas avoir d'effet d'amplification des pullulations de scolyte dans les parties gérées. Dans un contexte de changement climatique où la fréquence et l'intensité des perturbations sont modifiées voire amplifiées (Dobor et al., 2020a; McDowell et al., 2020; Samaniego et al., 2018; Seidl et al., 2017; Senf and Seidl, 2021b), la recherche de pratiques de gestion préservant la résilience forestière constitue un enjeu majeur.

8.4.6 Les limites de notre travail bibliographique

Nous avons cherché à analyser le bilan économique des coupes sanitaires, c'est-à-dire le bilan entre le bénéfice économique à exploiter les morts et déperissants et les coûts et pertes potentiellement engendrés. Ce bilan s'avère difficile à établir dans les faits, tant il peut varier selon l'échelle considérée, de la parcelle forestière à la filière. Dans une étude, Eklund, Wing et Sessions (2009) montrent qu'après un incendie, l'exploitation de l'ensemble des chandelles n'est pas le meilleur choix économique, à cause du coût engendré par l'exploitation des arbres éloignés des chemins de débardage par exemple. Ils invitent donc, dans une recherche de compromis avec le maintien d'habitat pour les oiseaux cavicoles, à maintenir toutes les chandelles sur les 50% de la parcelle les plus éloignées des chemins de débardage. Après une tempête, Iranparast Bodaghi et al. (2018) montrent que dans les forêts de montagne, les coupes sanitaires sont moins productives que l'exploitation traditionnelle, se traduisant par des coûts d'exploitation plus importants (de 10 à 30% plus élevés que la recette de vente du bois). À plus large échelle spatiale et temporelle, les coupes sanitaires et l'arrivée massive de bois exploités peuvent causer de fortes instabilités des marchés régionaux (Zhai and Kuusela, 2020). Il apparaît que les considérations économiques sur la gestion des peuplements perturbés sont rares, de même que sur l'effet des coupes sanitaires dans la survenue des épidémies ultérieures de ravageurs (voir 8.4). Il serait nécessaire d'étudier le bilan économique de telles opérations sanitaires à différentes échelles : de la parcelle de gestion forestière au marché régional, national, voire international. Néanmoins, l'absence de gestion induit l'abandon de l'ensemble des arbres du peuplement. Des scénarios intermédiaires doivent être étudiés avec, par exemple, le prélèvement des bois de plus grandes valeurs économiques et la conservation du reste du peuplement forestier. Cependant, plus globalement, il apparaît que la réalisation d'un bilan économique complet est difficile à réaliser, tant les facteurs à prendre en compte sont nombreux. Un bilan économique complet devrait intégrer à la fois les coûts directs liés aux opérations sanitaires, les coûts indirectes liées aux déstabilisations potentiels des marchés régionaux, voire nationaux mais aussi, ceux liés aux altérations des caractéristiques physico-chimiques des sols (i.e. baisse de fertilité, tassement, voir 8.4) et ceux liés à l'altération des communautés écologiques et les conséquences potentielles sur la résilience des écosystèmes forestiers.

Par ailleurs, nous avons trouvé peu d'études discutant de l'aspect social, concernant les réactions vis-à-vis d'un milieu forestier perturbé ou l'acceptation des coupes sanitaires par les visiteurs et/ou les riverains. Kortmann et al. (2021) montrent que des peuplements d'épicéas communs au sein de différentes zones protégées en Europe subissant des dépérissements très sévères causés par des infestations de typographes, conservent un haut niveau récréatif auprès des visiteurs. Dans ce cas, des coupes sanitaires visant à rendre le milieu plus acceptable auprès du public seraient relativement inefficaces (Kortmann et al., 2021). Cependant, dans une étude canadienne, McFarlane, Stumpf-Allen et Watson (2006) rapportent des réponses majoritairement hostiles d'habitants vivants à proximité de zones infestées par des scolytes (*Dendroctonus ponderosae*). Ces résultats contrastés et le peu d'études sur le sujet impliquent que ce champ de recherche soit approfondi.

Enfin, par la méthode utilisée, le comptage de votes ("*vote-counting*"), les conclusions de notre travail ont certaines limites. La principale limite est que nous ne pouvons pas pondérer notre analyse par l'incertitude et la magnitude des effets des coupes sanitaires associés à chaque étude. C'est d'ailleurs pour cela que nous avons cherché à considérer les résultats issus des différentes méta-analyses existantes sur le sujet dans notre discussion. La méta-analyse est une méthode quantitative de synthèse des résultats,

intégrant ces notions de magnitude et d'incertitude, fournissant donc des résultats plus robustes. Comptage de votes et synthèse narrative livrent une perspective globale sur un sujet dont le faible nombre d'études rend la méta-analyse impossible ou fragile.

8.5 Conclusion - Nécessité d'une réflexion holistique pour la gestion des peuplements déperissants

L'objectif de cette revue systématique de la littérature était de dresser le bilan de près de 30 ans de publications scientifiques internationales sur les effets des coupes sanitaires. Nous avons cherché à exposer l'ensemble des conséquences, positives ou négatives, des coupes sanitaires sur différents éléments déterminant la résilience des écosystèmes forestiers avec l'objectif d'éclairer au mieux les gestionnaires sur le choix de gestion des peuplements déperissants. Les coupes sanitaires induisent globalement une baisse de résilience dans les écosystèmes forestiers perturbés. Du point de vue de la biodiversité, les coupes sanitaires entraînent un recul des assemblages d'espèces vers des stades de succession plus précoces. Du point de vue de la régénération forestière, les coupes sanitaires n'induisent pas d'effet sur le succès global, bien qu'elles semblent défavoriser les espèces de fin de succession. Il semble que ces conséquences des coupes sanitaires résultent de l'extraction d'héritages biologiques tel que le bois mort, éléments issus du peuplement pré-perturbation et transformés par la perturbation. Les coupes sanitaires induisent aussi une plus forte ouverture du milieu forestier, une moindre fertilité et un plus fort tassement des sols. Par ailleurs, il apparaît que les coupes sanitaires augmentent le risque d'incendie ultérieur à court terme mais le réduisent à plus long terme. En revanche, ses effets sur les pullulations de ravageurs restent à préciser à l'aide de nouvelles études. Enfin, les coupes sanitaires paraissent avoir des effets relativement délétères sur les caractéristiques physico-chimiques des sols, en induisant du tassement, une perte de porosité, et de moindres capacités trophiques. Cependant, ces résultats concernant les sols sont issus d'une majorité de résultats étudiant les conditions après incendie. De nouvelles études sont donc nécessaires pour étudier les conséquences des coupes sanitaires sur les sols suite à d'autres perturbations naturelles (e.g. pullulation de ravageur, sécheresse, tempête, etc.). Enfin, en liaison avec le manque d'études dédiées, il est aujourd'hui difficile de conclure quant aux bénéfices économiques et sociaux que procurent les coupes sanitaires. Dans le cadre actuel des connaissances, le compromis entre objectif économique ("salvage"), objectif sanitaire ("sanitation") et objectif environnemental, semble difficile à trouver, tant les objectifs de maintien des héritages biologique d'une part, et de prélèvement des arbres moribonds d'autre part sont éloignés les uns des autres.

Il est d'importance grandissante d'associer les différentes dimensions présentées ici dans l'étude et la gestion des peuplements déperissants. Nous invitons donc les praticiens forestiers à une gestion intégrative des enjeux sociaux et environnementaux. Par ailleurs, nous les encourageons à pratiquer une gestion adaptative, telle que définie par Cordonnier et Gosselin (2009), c'est-à-dire une gestion "*qui s'appuie sur l'apprentissage en adaptant les pratiques en fonction de ce qui a été appris*". Dans un but de connaissance, l'évolution des écosystèmes forestiers déperissants, qu'ils soient exploités ou non, doit être étudiée en profondeur afin d'adapter la gestion et d'assurer leur meilleure résilience future. En attendant, la gestion actuelle peut déjà s'inspirer du corpus de connaissances disponibles dont nous avons cherché à faire la synthèse dans cet article.

Part VI

General discussion

Conséquences des dépérissements en forêts tempérées sur les structures d'habitat et la biodiversité : synthèse des résultats de thèse et apports de la littérature existante

9.1 Synthèse des résultats de la thèse - quelles sont les conséquences des dépérissements sur les structures d'habitats et la biodiversité

Les dépérissements forestiers sont à la croisée des chemins des grands enjeux écologiques du XXI^e siècle : changements climatiques, enjeux socio-économiques et protection de la biodiversité. Tout au long de cette thèse, nous avons souhaité accumuler des connaissances nouvelles afin de toujours mieux comprendre et prédire les conséquences actuelles de ces épisodes de dépérissement sur les écosystèmes forestiers et leur biodiversité associée, dans l'objectif d'améliorer les interventions humaines à leur égard. Pour cela, nous nous sommes appuyés sur trois cas d'étude européens ainsi que la littérature existante autour de ce sujet. Dans un premier temps, nous avons cherché à comprendre les conséquences de ces dépérissements sur les structures d'habitats au sein des forêts européennes, majoritairement gérées par l'homme (partie II). Par la suite, dans l'hypothèse que les changements d'habitat observés devraient affecter la biodiversité forestière, nous avons étudié l'effet des filtres environnementaux créés par les contextes de dépérissement post-perturbation, à l'échelle locale d'abord (partie III), puis à l'échelle paysagère (partie IV), sur les assemblages locaux de coléoptères saproxyliques. Enfin, nous avons souhaité étudier les conséquences des méthodes de gestion majoritaires des dépérissements, i.e. les coupes de récupération et sanitaires, sur des caractéristiques de la résilience forestière, dont la biodiversité (partie V).

9.1.1 Conséquences des dépérissements sur les structures d'habitats

Bois mort

Le dépérissement forestier étant le processus décrivant la mort progressive des arbres d'un peuplement forestier, nous avons de fortes hypothèses d'augmentation de cette ressource consécutivement à ce premier. Les différents résultats de thèse confirment cette hypothèse. Le dépérissement induit une augmentation significative de la ressource bois mort. Nous avons pu mettre en avant cette relation tant

sur nos différents cas d'étude que sur le jeu de données européen ICP Forest. Cependant, nous mettons aussi en avant que la ressource bois mort est multiple. Le bois mort n'est pas une simple matière inerte et homogène, il évolue dans le temps au fur et à mesure de sa colonisation par différentes communautés de micro-organismes et d'arthropodes. En réalité, il revêt une multitude de formes : selon son état de décomposition, selon l'espèce de l'arbre, selon son diamètre ou encore selon sa position et son exposition. Nos résultats traduisent cette multiplicité. Le dépérissement, alors qu'il est de valeur similaire en sapinières et en chênaies (Fig. 6.3), induit des changements différents dans chaque contexte (chapitre 4). En sapinières et pessières, l'augmentation se concentre sur le bois mort très décomposé. Au contraire, en chênaies, l'augmentation est plutôt concentrée sur le bois mort faiblement décomposé. On constate ici que l'espèce de l'arbre mort joue un rôle important dans le profil de décomposition post-dépérissement. Les chênes inventoriés (*Q. petraea* et *Q. robur*) sont connus pour leurs bois de cœur distinct et contenant de nombreux métabolites spécialisés, composés récalcitrants à longue décomposition (Harmon et al., 2020; Kahl et al., 2017). Par ailleurs, les perturbations, facteurs déclencheurs du dépérissement, apparaissent aussi comme des facteurs fondamentaux modulant les modifications d'habitat. Les tempêtes suivies d'épidémies d'*Ips typographus* dans les pessières bavaroises ont induit des augmentations de stocks de bois mort significativement plus fortes que les sécheresses en sapinières et chênaies françaises.

En outre, nous n'observons pas les mêmes changements de composition de types d'éléments ligneux (i.e. comprenant à la fois les arbres vivants et les arbres morts) selon le contexte considéré. Nous observons un changement significatif dans les sapinières pyrénéennes ($p < 0.01$; Tab. S4.2) mais pas dans les chênaies. La forte augmentation du bois mort dans les pessières et les changements significatifs de composition dans les sapinières d'une part, ainsi que les effets du dépérissement moins élevés en chênaies qu'en sapinières d'autre part, sont à mettre en regard des effets plus significatifs des dépérissements dans les forêts de conifères que dans les forêts de feuillues, que nous observons à l'échelle européenne (Tabs. S3.3, S3.4 et S3.5). Cette plus forte sensibilité des espèces de conifères en comparaison des espèces feuillues peut trouver son explication au travers de deux mécanismes. (i) À l'échelle européenne, les espèces de conifères ont historiquement connu des plantations monospécifiques hors de leurs aires naturelles de distribution en raison de leur forte productivité. Par exemple, en France, des plantations de *Picea abies* ont été largement mises en œuvre en plaine tout au long du XX^{me} siècle. Dans un contexte climatique où les sécheresses sont de plus en plus fréquentes et intenses, ces forêts se retrouvent au cœur des enjeux de résilience. La présence hors de leurs aires de distribution les rend très sensibles aux climats changeants alors que leurs peuplements monospécifiques les rendent d'autant plus sensibles aux perturbations biotiques (e.g. épidémies d'insectes xylophages; de Groot et al., 2019; Jactel et al., 2017, 2021). Nous constatons d'ailleurs que l'augmentation du bois mort en réponse au dépérissement en Europe, est principalement concentrée sur les espèces des genres *Pinus* et *Picea*, les deux genres de conifères les plus largement distribués en forêts productives de plaine en Europe (Barbati et al., 2006). (ii) De plus, le processus de dépérissement des arbres est apparu plus rapide dans nos cas de forêts de conifères, les pessières en raison du caractère éruptif des épidémies d'*I. typographus* après tempête (Kausrud et al., 2012; Müller et al., 2008), les sapinières en raison de la faible adaptation d'*A. alba* aux sécheresses (Lebourgeois et al., 2010).

Cependant, nous remarquons que les peuplements de chênes parmi les essences feuillues concentrent la majorité des effets des dépérissements sur le bois mort, avec des magnitudes d'effets proches de celles observées sur les genres *Picea* et *Pinus* (Tab. S3.3), et même supérieures concernant le bois mort peu carié (i.e. "fresh dead wood", Tab. S3.4). Le moindre effet du dépérissement dans notre cas d'étude ligérien est certainement le résultat de la pratique de coupes de récupération dans les chênaies étudiées fortement dépérissantes, la valeur commerciale des arbres dans ces parcelles étant élevée. Elle peut aussi être le résultat d'un effort d'échantillonnage moins élevé en chênaies que sur les autres cas d'études, induisant une plus forte variabilité statistique.

Enfin, d'après nos résultats, le dépérissement hétérogénéise la ressource ligneuse, tant vis à vis

de son niveau de décomposition que de son positionnement vertical. Plus globalement, il induit une augmentation de la diversité de types de bois mort local (Figs. 6.5, 6.6 et 6.7). À une échelle plus globale, le dépérissement induit une plus grande hétérogénéité des éléments ligneux d'un site à l'autre. En revanche, à travers l'augmentation globale des quantités de bois mort, il mène à une homogénéisation paysagère de cette seule ressource (Fig. S4.7). Ainsi, là où le bois mort est distribué de manière relativement aléatoire dans les forêts gérées non perturbées, il augmente en quantité et diversité sur tous les sites de la même façon suite à dépérissement, menant à une homogénéisation à l'échelle paysagère (Fig. SS6.1).

Dendromicrohabitats

De même que pour le bois mort, le dépérissement affecte les assemblages de dendromicrohabitats (DMHs) dans les sapinières pyrénéennes mais non dans les chênaies du Val de Loire (Tab. S4.2). Cependant, il conduit à une augmentation significative dans les deux cas d'étude, du nombre d'arbres porteurs de fructifications de champignons saproxyliques (Fig. S4.4). Ce développement de champignons lignivores résulte certainement de l'affaiblissement des arbres dépérissants, de la formation de surfaces sensibles à la colonisation par des champignons et des insectes et à terme, de leur mort (Kozák et al., 2018; Larrieu and Cabanettes, 2012). On observe d'ailleurs dans les sapinières une augmentation du nombre d'arbres porteurs de cicatrices laissant apparaître l'aubier et le bois de cœur (Fig. S4.4, Tab. S4.3). Par ailleurs, nos résultats montrent des corrélations matricielles significatives entre les éléments ligneux et les DMHs, tant en sapinières que dans les chênaies. Les DMHs étant portés par définition par des arbres, les changements concernant ces derniers affectent par extension les DMHs. Par exemple, Spínu et al. (2022) ont montré que les arbres vivants de gros diamètre et les arbres morts portent des compositions de DMHs différentes. Notre modèle d'équations structurelles (*SEM*; Fig. S4.8), montre les liens directs existant entre les arbres et les DMHs. Cette approche nous permet de mettre en avant des liens de causalité peu visibles par les approches de modélisation mettant en relation le dépérissement avec les structures d'habitat. Par exemple, nous montrons que l'augmentation du volume de bois mort fortement décomposé dans les sapinières, due au dépérissement, induit la plus forte présence de DMHs à développement lent. Pourtant, le dépérissement induit aussi une plus forte présence de DMHs à développement rapide (Fig. S4.5). Cette dernière relation signifie que la baisse d'ontogénèse des DMHs due au dépérissement l'est par une variable que nous n'avons pas mesurée dans le cadre de notre plan d'échantillonnage. Nous manquons par exemple de variables décrivant le microclimat forestier (e.g., températures, luminosités, ouverture de la canopée, etc.). Nous pouvons faire l'hypothèse que ce dernier, lui aussi largement affecté par le dépérissement (Kopáček et al., 2020), pourrait affecter la formation des DMHs. C'est le cas par exemple des bryophytes et des lichens qui ont un développement lent et de préférence dans des milieux humide et relativement ombrageux (Ranius et al., 2008), et sont donc certainement négativement affectés par le dépérissement.

De surcroît, nos résultats montrent que le dépérissement a eu pour conséquence d'augmenter l'hétérogénéité des DMHs d'un site à l'autre (i.e. à travers le paysage). Cette hétérogénéisation paysagère semble être le seul mécanisme expliquant l'augmentation de la diversité γ des DMHs dans les placettes dépérissantes, que ce soit dans les chênaies ou dans les sapinières (Fig. S4.3), puisqu'en parallèle, nous n'observons pas d'augmentation de la diversité α locale (Fig. S4.4). Cette hétérogénéisation paysagère pourrait avoir des effets bénéfiques sur la biodiversité puisqu'elle entraînerait une plus grande diversité globale de DMHs dans les milieux perturbés (Basile et al., 2020; Martin et al., 2022). Elle est à mettre au regard de la même hétérogénéisation des éléments ligneux (comptant à la fois les arbres vivants et le bois mort; Fig. S4.6).

Forêts dépérissantes : vers des attributs de vieilles forêts ?

Le dépérissement étant le processus décrivant la mort plus ou moins rapide et graduelle des arbres d'un peuplement forestier, nous pouvons nous questionner sur les similitudes entre ce processus et

celui de la sénescence naturelle des arbres due à leur âge. La question sous-jacente est alors de savoir si les forêts dépérissantes arborent des attributs classiquement associés aux vieilles forêts (*old-growth forests*)? Malgré la diversité écologique de ces vieilles forêts (Martin et al., 2018), elles partagent plusieurs caractéristiques communes : les arbres y sont relativement âgés (e.g., présence de gros vieux arbres vivants) et ces forêts sont composées d'espèces et d'habitats particuliers (e.g., présence d'espèces végétales de fin de succession, de nombreuses pièces de bois mort debout et au sol le long d'un large gradient de décomposition) (Wirth et al., 2009). La plupart des exemples de vieilles forêts dans les régions tempérées sont issus des réserves forestières strictes composées de forêts anciennement gérées et dans lesquelles toutes actions de gestion ont été prohibées, ou par des forêts présentes dans des milieux relativement inaccessibles, à faible rentabilité économique (Bouget et al., 2014b; Thompson et al., 2022b).

Nous avons établi dans nos différents cas d'étude les conséquences positives des dépérissements sur la ressource bois mort, tant en quantité globale que dans sa multiplicité. Cette forte quantité et diversité de bois mort est aussi une composante des forêts anciennes (Bouget et al., 2014b; Burrascano et al., 2013; Larrieu et al., 2012; Thompson et al., 2022b; Wirth et al., 2009). En revanche, tandis que la composition du bois mort en vieille forêt est généralement dominée par des pièces de diamètre élevé (Nilsson et al., 2003), nous n'observons aucun effet des dépérissements sur le diamètre moyen du bois mort.

Les vieilles forêts concentrent généralement une plus grande diversité de DMHs que les forêts gérées (Asbeck et al., 2022; Paillet et al., 2017; Thompson et al., 2022b; Winter and Möller, 2008). Toutefois, cette diversification des DMHs est moins prononcée que l'augmentation des quantités de bois mort (Bouget et al., 2014b). En revanche, dans nos cas d'étude, nous n'avons pas observé d'augmentation de l'abondance ou de la diversité des DMHs en réponse au dépérissement. La diversification généralement observée des DMHs dans les vieilles forêts est principalement due à la présence d'arbres vivants de très gros diamètres (généralement, des arbres de diamètre à 1,30 m supérieur à 67,5 cm; Larrieu et al., 2012; Paillet et al., 2017, 2019). Cette absence de diversification est certainement le résultat, en chênaies et sapinières, de l'absence (attendue) de différences de densités de ces arbres vivants de très gros diamètre selon le niveau de dépérissement. En pessière, nous observons des effets antagonistes dus au dépérissement : ce dernier a favorisé la quantité du bois mort de gros et très gros diamètre influençant positivement l'hétérogénéité des différents traits de DMHs, mais en parallèle a négativement affecté la diversité de DMHs en altérant la richesse des traits du bois mort. En revanche, en pessières, les tempêtes suivies d'épidémies d'*I. typographus* ont principalement affecté les arbres vivants de très gros diamètre, que l'on retrouve sous forme de bois mort après dépérissement, et qui sont considérés comme des attributs caractéristiques des vieilles forêts. Cette réduction est certainement le résultat des perturbations en action dans ce cas d'étude : on sait que les mortalités d'arbres dues à des tempêtes et des épidémies de scolytes sont régies par des effets seuils. Les arbres sont majoritairement renversés par les tempêtes après avoir dépassé une hauteur seuil (Gardiner and Quine, 2000; Jahani and Saffariha, 2021; Lohmander and Helles, 1987), et il en est de même avec les colonisations d'*I. typographus* s'installant sur des arbres ayant dépassé un diamètre à hauteur de poitrine d'environ 20-25 cm (Hlásny et al., 2021a).

Par ailleurs, les dépérissements ont pu induire des modifications d'assemblages de DMHs ou du moins, en favoriser certains, comme ce qui peut être observé dans les vieilles forêts. Par exemple, en sapinières et pessières, il a induit des changements significatifs d'assemblages là où en chênaies, il a favorisé l'abondance d'arbres porteurs de champignons pérennes (de même en sapinières avec les champignons éphémères, et en pessière). D'ailleurs, nous avons observé une augmentation de la quantité de DMHs saproxyliques (i.e. ceux contenant du bois mort en voie de décomposition) en réponses aux dépérissements en sapinières. Dans une étude portant sur les déterminants de la présence des DMHs dans des réserves forestières françaises, Paillet et al. (2019) ont montré que les plus fortes occurrences d'arbres vivants de gros diamètre et d'arbres morts favorisaient plus fortement les DMHs liés aux processus de décomposition du bois que les autres. Par conséquent, bien que nous n'ayons pas observé de diversification des DMHs suite au dépérissement comme nous pouvons l'observer dans les vieilles forêts, nous avons pu mettre en

évidence un changement de leurs assemblages au profit de DMHs saproxyliques dans le cas des sapinières, se rapprochant des phénomènes observés dans les réserves forestières françaises (Paillet et al., 2019). De même, l'augmentation ou du moins, la présence indicatrice du nombre d'arbres porteurs de fructifications de champignons lignicoles dans les forêts dépérissantes peut être un autre critère de similitude avec les forêts anciennes (Bouget et al., 2014b; Winter and Möller, 2008). Ce DMH, directement lié au processus de décomposition du bois, est caractéristique des arbres sénescents, et est généralement soustrait lors des actions de gestion forestière en raison de la dégradation du bois de cœur que le champignon induit (Larrieu et al., 2012; Winter and Möller, 2008).

En conclusion, les similitudes entre forêts dépérissantes et vieilles forêts sont principalement le résultat de l'augmentation des quantité et diversité du bois mort suite à la mortalité des arbres (Bouget et al., 2014b). En outre, nous avons pu observer des similitudes dans les réponses des assemblages de traits de DMHs (i.e. principalement le trait saproxylique en sapinières ; Paillet et al., 2019). Cependant, l'absence d'arbres vivants de très gros diamètres est un caractère différenciant fortement les forêts dépérissantes des vieilles forêts. Ceci explique aussi certainement l'absence de diversification de DMHs dans les forêts dépérissantes. De surcroît, la baisse significative de surface terrière des arbres vivants peut faire craindre, au contraire d'un vieillissement, un rajeunissement à long terme si les perturbations naturelles sont fréquentes et/ou sévères, conduisant à de fortes mortalités dans les peuplements forestiers (McDowell et al., 2020).

9.1.2 Effets des dépérissements sur les assemblages de coléoptères saproxyliques

Comme nous l'avons mentionné en introduction de ce manuscrit, les coléoptères saproxyliques composent un groupe écologique menacé en Europe (Calix et al., 2018; Hagge et al., 2021; Seibold et al., 2015). Cet état est principalement le résultat de l'historique de pression anthropique sur les forêts ayant conduit à la réduction de la quantité et/ou diversité du bois mort et des DMHs en comparaison des forêts à dynamiques naturelles (Asbeck et al., 2022; Bouget et al., 2014b; Larrieu et al., 2012, 2014; Martin et al., 2021; Siitonen, 2001). Par conséquent, nous avons montré que la promotion du bois mort et des DMHs liés à la décomposition du bois (i.e. dits "saproxyliques") en raison des épisodes de dépérissements, ont pu bénéficier aux communautés de coléoptères saproxyliques et ce, à travers différents mécanismes que nous allons détailler.

Les effets des dépérissements à l'échelle locale

La littérature décrit généralement une réponse positive des coléoptères saproxyliques aux perturbations naturelles et dépérissements induits (Beudert et al., 2015; Boucher et al., 2012; Kozák et al., 2021; Viljur et al., 2022). Nos résultats montrent que localement, les coléoptères saproxyliques peuvent favorablement répondre au dépérissement en raison des modifications d'habitats et de ressources. Nous avons émis l'hypothèse que la réponse locale des coléoptères saproxyliques résulte de deux mécanismes potentiels : (i) la diversité α résulterait de l'effet direct de l'hétérogénéité des habitats (i.e. "*hypothèse d'hétérogénéité d'habitat*", "*habitat-heterogeneity hypothesis*") (Hutchinson, 1957; Seibold et al., 2016), ou (ii) la diversité α résulterait de l'augmentation du nombre d'individus causée par une plus grande quantité de ressources disponibles (i.e. "*hypothèse du lien espèce-énergies*", "*species-energy hypothesis*"). La première associe donc les changements de diversité α à la diversité d'habitats, l'autre à la quantité de ressource.

Nos premiers résultats nous ont conduit à considérer plutôt l'importance de la quantité de ressource disponible. En effet, en pessières, nous avons observé une nette réponse de l'abondance et de la richesse spécifique des coléoptères saproxyliques au bois mort debout (Chap. 5, Tab. 5.4). Toutefois, au delà de la quantité de ressource, le bois mort debout abrite de nombreuses niches en raison d'une grande hétérogénéité verticale, tant microclimatique que physique (e.g., diamètres différents de la base à l'apex), et horizontale (i.e. exposition au soleil). Cette diversité de niches semble permettre la coexistence d'une

grande richesse d'organismes saproxyliques (Bouget et al., 2012, 2014a; Sverdrup-Thygeson and Ims, 2002). En outre, nos résultats ont montré que le nombre de pièces de gros bois mort au sol participait lui aussi à augmenter la richesse spécifique locale des coléoptères saproxyliques. Néanmoins, dans les sapinières, nous n'avons observé que peu de réponses des coléoptères saproxyliques aux gradients environnementaux étudiés (Tab. 5.3). La réponse des organismes saproxyliques à des augmentations des quantités de bois mort, n'est pas linéaire (Müller and Büttler, 2010). Le dépérissement induit par des sécheresses en sapinière était nettement moins sévère que celui en pessière, conduisant à une moindre augmentation des quantités de bois mort, certainement inférieure au seuil nécessaire pour une réponse significative de la communauté des coléoptères saproxyliques.

Par ailleurs, nos résultats en pessière ont montré des changements dans les communautés de coléoptères saproxyliques en réponse au dépérissement, en lien avec les préférences des insectes pour certains types de bois mort. Ainsi, les communautés présentes dans les placettes fortement dépérissantes avaient des préférences pour du bois mort de plus gros diamètre et plus fortement décomposé que celles présentes dans les placettes non dépérissantes. D'après les résultats de Gossner et al. (2013), ces changements de traits fonctionnels au sein des communautés de coléoptères saproxyliques sont généralement observés en réponse à de fortes rétentions de bois mort dans les parcelles forestières gérées. À l'aide d'analyses complémentaires, nous avons montré que dans les placettes étudiées, les espèces ayant des préférences pour du bois mort de plus gros diamètre sont aussi plutôt des espèces saproxyliques classées comme étant menacées sur liste rouge. De même, à partir d'une table de traits multi-espèces, Seibold et al. (2015) ont montré que les espèces de coléoptères saproxyliques menacées sur liste rouge sont les plus grandes et celles colonisant le bois mort de gros diamètre. Ainsi, au travers des augmentations de quantité du bois mort debout, le dépérissement des pessières a favorisé des espèces saproxyliques actuellement menacées.

Enfin, de nouvelles analyses ont montré que les conséquences des dépérissements sur les éléments ligneux, dont le bois mort, ont eu de fortes conséquences en cascade sur les DMHs dans les forêts de conifères étudiées. C'est en grande partie ces modifications en cascade des DMHs dans les sapinières et pessières, qui ont induit des changements de diversité α chez les communautés de coléoptères saproxyliques. Par exemple, on voit qu'en sapinières, la richesse spécifique a bénéficié de l'augmentation de DMHs saproxyliques tandis qu'en pessières, c'est la réduction de la durée de vie des DMHs qui a favorisé la richesse spécifique. Néanmoins, en pessières, la divergence fonctionnelle bénéficie directement de l'augmentation de quantité de bois mort de gros à très gros diamètre. À l'échelle des assemblages taxonomiques et fonctionnels de coléoptères saproxyliques, au sein de nos trois cas d'étude, les gradients environnementaux significatifs dans leur structuration sont soit associés à des variables de diversité du bois mort (e.g., diversité et richesse de traits du bois mort), soit des variables de DMHs, décrivant par définition des modifications de niches disponibles dans les environnements étudiés. Par conséquent, ces derniers éléments nous amèneraient à plutôt considérer les réponses locales des coléoptères saproxyliques aux changements d'habitats et de ressources, sous le prisme de l'hypothèse d'hétérogénéité d'habitat (Seibold et al., 2016). C'est à des gradients d'hétérogénéité et de disponibilité des habitats, affectés ou non par le dépérissement, que répondent dans nos cas d'études les communautés de coléoptères saproxyliques.

Les effets des dépérissements à larges échelles

Les coléoptères saproxyliques ont globalement de bonnes capacités de dispersion, pouvant parcourir d'une centaine de mètres jusqu'à plusieurs kilomètres afin de trouver habitat, ressource et/ou partenaire potentiel (Bergman et al., 2012; Jonsell et al., 1999; Komonen and Müller, 2018; Miguet et al., 2016; Økland et al., 1996; Ranius, 2006). Par extension, les seules mesures de quantité de ressources locales peuvent masquer les dynamiques de colonisation et d'extinction dus aux distances plus ou moins importantes entre patchs d'habitats (MacArthur and Wilson, 1967; Økland et al., 1996). Par conséquent, loin de ne répondre qu'à des quantités d'habitat concentrées en un site, les coléoptères saproxyliques échantillonnés en ce site particulier peuvent répondre en réalité à une quantité d'habitat global présent

dans le "paysage local". C'est à mettre en lien avec les échelles d'effet ("*scale of effect*") qui appartiennent à chaque espèce ou groupe d'espèce et dépendent du contexte d'étude. Elles décrivent l'entité géographique dans laquelle la communauté considérée peut se déplacer; [Fahrig, 2013](#); [Jackson and Fahrig, 2015](#); [Miguet et al., 2016](#)). L'importance de la quantité d'habitat dans un paysage local, reliant en un les concepts de taille et d'isolement des îles, est décrite par l'hypothèse de la quantité d'habitat (*habitat-amount hypothesis*; [Fahrig, 2013](#)). Par exemple, [Økland et al. \(1996\)](#) ont montré que les coléoptères saproxyliques répondent majoritairement à des facteurs environnementaux (i.e. quantité de bois mort et de fructifications de champignons lignicoles) mesurés à de larges échelles spatiales (i.e. de un à quatre km²).

En ce sens, [Seibold et al. \(2017\)](#) ont expérimentalement testé l'hypothèse de la quantité d'habitat sur la richesse spécifique des coléoptères saproxyliques. Ils ont déterminé le paysage local comme étant compris entre 40 et 120 m de rayon. De même, [Haeler et al. \(2021\)](#) ont observé des réponses positives significatives et stables des coléoptères saproxyliques à l'augmentation des quantités de bois mort le long d'un gradient spatial allant de 20 à 200 m. Nous avons nous même calculé les quantités de canopée morte dans le cas de la sapinière afin de pouvoir déterminer une échelle de l'effet dans la réponse des coléoptères saproxyliques (Chap. 7). De même que les études citées précédemment, nous observons les réponses les plus fortes et significatives de la richesse spécifique locale au dépérissement mesuré dans un rayon de 200 m (Fig. 7.4). En revanche, nos résultats révèlent des réponses fortes des traits fonctionnels aux échelles paysagères. Ainsi, les espèces de grande taille, ayant des préférences pour du bois mort fortement décomposé et de gros diamètre bénéficiaient du dépérissement mesuré dans un rayon de 1500 m. Ces résultats pourraient expliquer l'absence de réponse des traits fonctionnels au dépérissement local dans les sapinières dans notre première étude, alors qu'ils répondent significativement et positivement dans les pessières bavaroises. Le dépérissement en pessière ne fût pas sévère que localement mais à de large échelles spatiales : [Müller et al. \(2008\)](#) nous apprennent que dans la même zone géographique d'étude, la taille globale moyenne des trouées causées par le dépérissement des arbres suite à des épidémies d'*I. typographus* est de 6,8 ha. Ainsi, les conditions locales reflétaient aussi les conditions paysagères. Il est donc très probable qu'en réalité, les réponses locales de traits observées en pessières soient le résultat de processus paysagers. Par exemple, la taille des espèces est parfois utilisée comme proxy de leurs capacités de dispersion, trait fonctionnel principalement affecté par des processus macroécologiques tel que la composition des habitats d'un paysage ([Dufлот et al., 2014](#)). De même, les processus d'homogénéisation biotique (i.e. le déclin de traits écologiques, principalement portés par des espèces spécialistes; [Clavel et al., 2011](#)) semblent être principalement le résultats de processus globaux, mesurés à des échelles paysagères ([Gámez-Virués et al., 2015](#)).

Afin de mieux considérer la distribution des espèces dans le paysage, en réponse au dépérissement, nous avons étudié la diversité β des coléoptères saproxyliques et sa décomposition en composantes de remplacement (i.e. *turnover*) et de richesse (i.e. *gain/loss*; [Baselga, 2010](#); [Cardoso et al., 2014](#); [Carvalho and Cardoso, 2020](#)). Nous avons alors émis l'hypothèse que l'augmentation globale de la quantité de bois mort en raison des dépérissements et son homogénéisation à l'échelle du paysage, malgré une hétérogénéisation des DMHs, devrait conduire à une homogénéisation des communautés de coléoptères saproxyliques. Cette homogénéisation peut se traduire par deux mécanismes sous-jacents : une baisse de diversité β parmi les placettes fortement dépérissantes, et/ou une augmentation de la composante de remplacement et une baisse de la composante de richesse de la diversité β . De plus, nous avons effectué ces analyses sur les compositions taxonomiques et fonctionnelles, en raison des réponses différentes de ces deux composantes de biodiversité que nous avons observées dans nos précédentes analyses (Chaps. 5 et 7). Par exemple, [Georgiev et al. \(2022\)](#) ont montré que suite à des tempêtes, la diversité β taxonomique des coléoptères saproxyliques a significativement baissé, traduisant une homogénéisation des communautés à l'échelle du paysage. Nous observons au travers de nos trois cas d'étude, des réponses similaires, avec en chênaies, une réduction significative de la diversité β intra-classe en réponse au dépérissement,

et en sapinières et pessières, une augmentation significative de la composante de remplacement et une baisse de la composante de richesse (Chap. 6). Cependant, nous avons observé des disparités de réponse des composantes de diversité β en sapinières et en pessières, avec des changements significatifs plutôt concentrés sur la composition fonctionnelle dans les sapinières alors qu'ils sont concentrés sur la composition taxonomique dans les pessières (Fig. 6.9). Dans les sapinières et pessières, cette augmentation de la composante de remplacement couplée à une augmentation de la diversité α , qu'elle soit taxonomique ou fonctionnelle, en raison de processus locaux ou paysagers, illustre un processus de généralisation des espèces et/ou traits saproxyliques dans le paysage sous l'effet des dépérissements. Par ailleurs, l'absence globale de changement des assemblages taxonomiques et fonctionnels (excepté en pessière pour les assemblages taxonomiques) renseigne sur l'absence de colonisations massives par de nouvelles espèces portant de nouvelles valeurs de traits fonctionnels, absentes des milieux peu ou non dépérissants. Cette absence de colonisation traduit probablement un phénomène de supplémentation de ressources dans le paysage : les ressources retrouvées dans les milieux dépérissants sont déjà présentes dans les milieux non dépérissants mais plus lâchement dispersées à travers le paysage. Par conséquent, en augmentant partout localement des ressources précédemment dispersées dans le paysage, le dépérissement a conduit à généraliser la présence des espèces de coléoptères saproxyliques et/ou des traits portés par ces derniers et qui étaient précédemment dispersées de la même manière que les ressources, dans le paysage.

9.1.3 Effets de la gestion anthropique post-dépérissement sur les assemblages de coléoptères saproxyliques

Nous avons montré que le dépérissement peut être favorable pour un certain cortège de la biodiversité forestière. Cependant, l'affaiblissement et la mortalité des arbres, a des répercussions économiques. Par ailleurs, les arbres infestés par des ravageurs opportunistes peuvent constituer des foyers de colonisation des arbres sains aux alentours. Les forêts tempérées sont généralement gérées afin de fournir des services aux sociétés humaines, par la production de bois par exemple. Ainsi, la réponse généralement apportée par la gestion forestière à ces épisodes de dépérissement est l'exploitation des arbres avant leur détérioration mécanique (i.e. coupe de récupération, "*salvage logging*") ou avant qu'ils ne servent de tremplin à de futurs épisodes épidémiques (i.e. coupes sanitaires, "*sanitation logging or felling*"). En plus du processus de dépérissement, ces coupes de récupération et sanitaires peuvent agir comme une perturbation supplémentaire sur l'écosystème forestier (Leverkus et al., 2018a). L'interaction ici en jeu entre la perturbation naturelle et celle anthropique inquiète les chercheurs écologues à travers le monde (Leverkus et al., 2018a; Lindenmayer et al., 2008; Müller et al., 2019).

Thorn et al. (2018a) ont montré, à travers une méta-analyse, les conséquences généralement négatives des coupes de récupération sur la biodiversité forestière. Dans les sapinières et pessières, nos résultats n'ont pas montré de baisse significative de l'abondance ou de la richesse spécifique des coléoptères saproxyliques (nous notons néanmoins une baisse significative de la richesse spécifique des espèces menacées sur liste rouge). Notre résultat le plus intéressant concernant les relations écologiques régissant les assemblages locaux de coléoptères saproxyliques. Là où sur le gradient de dépérissement, ces derniers répondent majoritairement à l'augmentation de la quantité de bois mort debout, les coupes sanitaires entravent cette relation : dans les zones ayant été exploitées suite à la perturbation, les abondances et richesses spécifiques restent artificiellement élevées dans ce contexte où la quantité de bois mort debout a été significativement réduite. Nous émettons une hypothèse de *dette d'extinction* pour expliquer ces niveaux relativement élevés de diversité saproxylique suite aux coupes de récupération. La dette d'extinction décrit les processus de retard de réponse d'un groupe écologique lié à un habitat particulier, suite à la perte de ce dernier (Kuussaari et al., 2009; Tilman et al., 1994). Par conséquent, la baisse significative de la richesse spécifique des coléoptères saproxyliques menacés sur liste rouge peut être envisagée comme un indice de début de paiement de cette dette d'extinction, par la disparition d'abord des espèces les plus sensibles aux changements d'habitat. De même, notre travail de revue de la littérature

a permis de mettre en avant les conséquences négatives des coupes de récupération et sanitaires sur la biodiversité forestière (Chap. 8).

Nous venons de présenter et discuter les résultats issus des travaux de la thèse. Les dépérissements étudiés, à l'échelle de nos cas d'étude ou à l'échelle européenne, ont eu pour conséquence d'augmenter les quantités et diversité de bois mort. Sur nos cas d'étude, nos résultats ont montré des modifications des assemblages de dendromicrohabitats. Ces changements d'habitat ont bénéficié en cascade aux assemblages de coléoptères saproxyliques.

Nos résultats s'intègrent dans une matrice d'enjeux et de contextes globaux, composés du changement climatique et des changements de régimes de perturbations en résultant, du déclin de la biodiversité, de l'homogénéisation biotique, de la sur-exploitation des écosystèmes : des sujets que nous avons déjà présenté en introduction de ce manuscrit et des chapitres de résultats. Nous avons souhaité élargir le propos de nos résultats en les réintégrant dans cette matrice d'enjeux et contextes globaux. Pour cela, au travers d'une revue de la littérature, nous avons étudié, les conséquences sur les communautés d'arthropodes, des principales perturbations abiotiques modulant les forêts tempérées (i.e. les sécheresses, les tempêtes et les feux de forêt). Nous nous sommes tout particulièrement concentrés sur l'importance des différents héritages de perturbations pour les communautés d'arthropodes post-perturbation. À cela, nous avons ajouté l'étude des effets des changements de régimes de perturbation, des conditions pré-perturbation et des méthodes de gestion post-perturbation. Cette revue présente ci-après a donc pour objectif d'inclure les résultats présentés précédemment dans cette perspective plus globale.

Conclusion et perspectives

Les perturbations naturelles sont des composantes majeures des écosystèmes forestiers. Elles structurent leur hétérogénéité spatiale, créent de nouveaux habitats et ressources, et régulent leur fonctionnement. Leurs régimes historiques ont façonné les paysages forestiers que nous observons aujourd'hui. Cependant, les changements globaux, qu'ils soient d'ordre climatique ou de l'ordre de l'utilisation des terres, induisent des modifications des régimes de ces perturbations. Ces changements ont des conséquences écologiques lourdes et pourraient mener certains écosystèmes forestiers vers des états non-boisés. Le processus de mort plus ou moins progressive des arbres d'un peuplement forestier est appelé *dépérissement forestier*. Dans ce cadre, nous avons étudié la réponse des structures d'habitat et des assemblages de coléoptères saproxyliques dans différents cas d'étude de dépérissements forestiers, principalement en forêts tempérées.

Nous avons pu mettre en évidence les effets favorables des dépérissements sur les stocks de bois mort, leur diversité et l'hétérogénéité des dendromicrohabitats dans le paysage. Ces changements d'habitat ont en cascade bénéficié aux assemblages de coléoptères saproxyliques, tant sous la forme taxonomique que fonctionnelle. Si la diversité taxonomique (i.e. en nombre d'espèces) semblait principalement répondre à des processus à relative petite échelle spatiale (i.e. un rayon de 200 m), la diversité fonctionnelle, par le biais des traits fonctionnels, répondait à de plus larges échelles spatiales (i.e. à un rayon de 1500 m). De même, la diversité phylogénétique profitait de l'hétérogénéité spatiale du dépérissement aux échelles paysagères. Par conséquent, nos résultats tendent à considérer les zones de forêts dépérisantes comme de potentielles zones favorables à la conservation d'espèces liées à des habitats rares en forêts gérées, comme le bois mort. Au contraire, nous avons pu montrer certains effets délétères des coupes de récupération et sanitaires sur la biodiversité forestière. Nous proposons ainsi d'utiliser des îlots de forêts dépérisantes comme réserves ponctuelles pour cette biodiversité menacée. Nous appelons aussi à considérer la distribution paysagère de ces îlots : si les coléoptères ont de bonnes capacités de dispersion, cela ne semble pas être le cas pour d'autres taxons saproxyliques, tels que les champignons ou les bryophytes, qui ont besoin d'îlots proches les uns des autres pour assurer leur dispersion dans le paysage (Haeler et al., 2021).

Enfin, nous insistons sur le caractère primordial des héritages biologiques dans la formation des communautés d'arthropodes post-perturbation. Nous insistons aussi pour l'intégration des travaux concernant les effets des perturbations et dépérissements sur la biodiversité, à des approches multi-taxonomiques (e.g., Kortmann et al., 2022; Sire et al., 2022), de comparaisons temporelles (e.g., Kozák et al., 2021) et spatiales (e.g., Cours et al., 2022). De même, les processus de changement de trajectoire écologique et de transformation d'écosystèmes forestiers en milieux non-boisés ont besoin d'être mieux compris. Les caractéristiques assurant la résilience de l'état boisé dans un contexte de changement environnemental

rapide, ont besoin d'être identifiées et étudiées pour assurer le maintien de la biodiversité associée à ces écosystèmes et la continuité des services écosystémiques profitant aujourd'hui aux sociétés humaines.

Ce manuscrit a été alimenté par l'accumulation de nouvelles connaissances et la synthèse de connaissances existantes dans la littérature. Tout cumul de nouvelles connaissances apporte en suivant de nouvelles questions de recherche. J'ai essayé ici de dresser une liste de ces nouvelles questions ou idées et approches.

- Il est nécessaire aujourd'hui de multiplier les cas d'études de réponses de la biodiversité aux épisodes de dépérissement, surtout vis-à-vis des perturbations émergentes en un lieu donné (e.g., les sécheresses en Europe). De même, il apparaît nécessaire d'adopter des approches multi-taxon afin de caractériser au mieux et dans une certaine exhaustivité les réponses de la biodiversité. Cela demande d'améliorer les bases génétiques mais aussi les bases de traits des espèces, tant l'approche fonctionnelle apparaît importante pour étudier les réponses biotiques (e.g., [Kortmann et al., 2022](#); [Sire et al., 2022](#)).
- La littérature a mis en évidence le rôle de catalyseur du changement et de l'adaptation tenu par les perturbations (e.g., [Dietz et al., 2020](#); [Thom et al., 2017b](#)). Il pourrait donc apparaître opportun de déterminer les niches de température de chacune des espèces de nos cas d'étude et déterminer si, à niveau égal de niche de fermeture de la canopée, les coléoptères saproxyliques capturés dans les milieux perturbés sont associés à des niches de température plus élevées.
- Dans un contexte de changement des régimes de perturbation, nous pouvons faire l'hypothèse que les différentes perturbations affectent différemment les communautés dans le temps. Là où la communauté d'un site particulier résulte d'un historique de perturbation, le changement de régime de perturbation actuel devrait induire des changements de communauté différents des perturbations passées. On peut donc faire l'hypothèse que si les changements de régimes de perturbation sont déjà assez forts, ils devraient pouvoir être observés au travers des communautés observées après perturbation : les assemblages d'espèces post-perturbation aujourd'hui devraient être différents des assemblages post-perturbation passés et ce changement devrait augmenter en remontant le temps, comme fonction des changements de régime de perturbation (certainement de manière exponentielle). On peut aussi questionner la magnitude des changements d'assemblages (la diversité β) entre milieux non-perturbés et milieux perturbés en fonction du temps, avec de moindres valeurs de dissimilarité dans le passé qu'aujourd'hui.
- En raison du changement climatique et de ces changements des régimes de perturbations, nous commençons à observer des feux de forêt plus fréquents au sein de forêts dont le régime de perturbation historique intègre peu d'incendies. Il apparaît important d'étudier les processus de colonisation et décomposition des arbres brûlés dans ces milieux en changement et de les comparer avec du bois mort issu des processus historiques de perturbation et des processus de sénescence. Il est alors attendu une colonisation par les seules espèces généralistes et opportunistes puisque le pool régional ne doit pas compter d'espèces spécialisées dans la colonisation de ces arbres brûlés. Il pourrait alors être comparé ces nouveaux processus de colonisation avec les processus de colonisation et décomposition des arbres brûlés dans des environnements historiquement perturbés par des feux et colonisé par des espèces spécialisées dont les traits ont été historiquement sélectionnés.

- Il apparaît important aujourd'hui de caractériser les changements de régime de perturbations, à identifier les cas de changements de trajectoires écologiques suites à une ou des perturbations et à les comparer avec des milieux proches (tant géographiquement qu'en terme de fonctionnement pré-perturbation) dans l'objectif d'identifier les caractéristiques ayant mené l'un vers le changement de régime écologique et l'autre dans le maintien de ses fonctions pré-perturbations (i.e. identifier les caractéristiques de résilience). Cela pourrait déjà faire l'objet d'une revue de la littérature ou d'une méta-analyse à partir des cas déjà documentés. Cela pourrait aussi être analysé à l'aide d'outils de simulation (e.g., [Turner et al., 2021](#)). De même, dans ce cadre, la question des points de bascule est à étudier en détail, i.e. à partir de quelle sévérité \times fréquence \times étendue spatiale de perturbation, un changement d'une trajectoire écologique à une autre est-il observé. Les mécanismes eux-mêmes régulant ces points de bascules sont à étudier afin de mieux prédire la survenue de ces changements et potentiellement adopter les meilleures stratégies de maintien de la résilience. Par ailleurs, il apparaît tout aussi important de comprendre les caractéristiques déterminant ces trajectoires écologiques et, tant qu'il y a maintien de l'écosystème d'origine, d'identifier à partir de ces caractéristiques le nombre et la direction des trajectoires alternatives et quels facteurs décident de l'emprunt d'une trajectoire particulière.

Appendices

Dieback effects on dead wood: large scale trends from cross-analysis of European forest databases

C. BOUGET , C. BARD, J. COURS 

Abstract

Deadwood is a particularly rare habitat in European managed forests, although it supports a high level of biodiversity. However, forest dieback, due to natural disturbances exacerbated by current climate change, could increase the stock of deadwood in managed forests. This increase is expected to depend on several factors associated with the disturbance, e.g. its intensity, or the forest stand, e.g. tree species or forest management.

We used a time series of annual defoliation surveys of European forests to characterise the dieback phenomenon. In addition, we used data from a study carried out between 2006 and 2009 on the amount of dead wood present on the same survey plots. The total amount of dead wood was broken down by diameter and decay. We focused on the ten years of defoliation survey before measuring dead wood in order to maintain a large number of survey plots.

We showed that the average level of defoliation in the five years prior to the deadwood survey increased the amount of deadwood. At the same time, the longer the time since the last defoliation peak, the less dead wood there was. However, these effects were concentrated on fresh deadwood, decayed deadwood was not affected by decay in the ten years prior to the measurement and therefore seems to require longer time series.

We shown that the stock of deadwood in European forests is significantly affected by dieback.

Keywords: Forest dieback; Dead wood; Biological legacy; Climate change

Résumé

Le bois mort est un habitat particulièrement rare dans les forêts européennes gérées alors qu'il abrite une grande biodiversité. Néanmoins, le dépérissement des forêts, dû à des perturbations naturelles exacerbées par le changement climatique actuel, pourrait augmenter le stock de bois mort dans ces forêts gérées. Cette augmentation devrait dépendre de plusieurs facteurs associés aux perturbations, e.g. leur intensité, ou au peuplement forestier, e.g. les espèces d'arbres ou la gestion forestière.

Nous avons utilisé une série chronologique d'enquêtes annuelles sur la défoliation des forêts européennes pour caractériser le phénomène de dépérissement. En outre, nous avons utilisé les données d'une étude réalisée entre 2006 et 2009, sur les quantités de bois mort présentes sur les mêmes placettes d'enquête. La quantité totale de bois mort a été déclinée en fonction du diamètre et de la décomposition. Nous nous sommes concentrés sur les dix années d'étude de la défoliation avant mesure du bois mort afin de maintenir un grand nombre de placettes.

Nous avons ainsi montré que le niveau moyen de défoliation dans les cinq années précédant le relevé du bois mort augmentait la quantité de bois mort. Parallèlement, plus le temps s'écoule depuis le dernier pic de défoliation, moins il y a de bois mort. Cependant, ces effets se sont concentrés sur le bois mort frais, le bois mort décomposé n'a pas été affecté par le dépérissement dans les dix années précédant la mesure et semble donc nécessiter de plus longues séries chronologiques.

Nous avons montré que le stock de bois mort dans les forêts européennes est significativement affecté par le dépérissement.

Keywords: Dépérissement forestier; Bois mort; Héritage biologique; Changement climatique

A.1 Introduction

In managed forest landscapes, dead wood volume is considered a weak point, although it is well acknowledged as an indirect indicator of biodiversity (Lassauce et al., 2011). Strategies to increase its primary level are consequently given special attention as part of environmentally sound management practices.

Across European forests, since the 1980s decade, natural disturbances have increased in extent, frequency, and severity, with climate change as the driver of consecutive droughts among other agents (Senf and Seidl, 2021b). Carnicer et al. (2011) reported a generalized increase in crown defoliation in response to increased water deficit in southern European forests occurring during 1987–2007. They found that defoliation trends are paralleled by significant increases in tree mortality rates. In forest ecosystems, drought-induced diebacks cause deep changes in forest composition and structure; by inducing branch and tree mortality, they increase the volume of dead wood as a biological legacy. Several case studies highlighted that local dead wood significantly increased with local and contemporary dieback level (Cours et al., 2021, 2022).

Whether and how a succession of repeated die-offs may affect dead wood stocks has not been studied. However historical ecology suggests that historical legacies may be prone to time-lagged, cumulative or lock-ins effects (Tappeiner et al., 2021). Using reconstructed disturbance history, Kozák et al. (2021) demonstrated that epiphyte lichen communities, strongly determined by old-growth features, were affected by the current forest structure and disturbance regimes over the past 250 years.

In this paper, we carried out an opportunistic correlative study between past crown conditions and dead wood volumes, and we investigated the structural effects of a succession of tree declines in European forests. In a subset of level I 16×16 km monitoring plots, we benefited from both dead wood measurements carried out in the framework of the ForestFocus Biosoil project (Galluzzi et al., 2019) and defoliation assessments yearly conducted in the context of surveys of crown condition. Based on the cross-analysis of these two large-scale European forest databases, we addressed the following questions. Are plot-level volumes of dead wood correlated to contemporary or near past levels of local dieback? If related to past dieback, is the dead wood stock more linked with extreme diebacks associated to severe disturbance events, or with high average defoliation level or high frequency of past defoliation? Across European forests, does the dead wood-dieback relationship vary with forest context (lowland vs highland, deciduous vs coniferous...)?

A.2 Materials and methods

A.2.1 ICP database and defoliation protocol

International Cooperative program on assessment and monitoring of air pollution effects on the forest (ICP Forests) is responsible for extensive level I monitoring system of forest sites (Haußmann and Fischer, 2004), which has been in operation since 1986. The large scale level I network is dedicated to investigations on forest condition monitoring and was built as a dense and spatially representative 16×16 km virtual grid of forest sampling points placed over Europe. This extensive network of observation points covers most of European forested areas with ca 6000 monitoring plots in 42 countries. In each European Level 1 plot, a visual evaluation of the defoliation and discoloration of tree crowns is performed annually to survey health status of European forests (icp-forests.net). Data management is presently carried out at the Programme Co-ordinating Centre (PCC) of ICP Forests in Eberswalde, Germany, where all data are available upon request. Since 1989, the standardized procedure of "annual surveys of crown condition" has been performed on 24 selected predominant, dominant and co-dominant individual trees, with a minimum height of 60 cm and without significant mechanical damage. The defoliation and discoloration level of each tree crown is visually assessed as the percentage of needle/leaf loss in the assessable crown as compared to a reference tree with full foliage, using a sliding scale of 5%. The mean defoliation at the plot scale is the proportion of trees scored as "damaged", i.e. with a defoliation rate of more than 25%, and is used as a proxy of plot dieback level. In the ICP database, factors associated with the observed defoliation about natural disturbances or management (vertebrate herbivory, insect herbivory, fungal damage, drought impacts, fire damage, signs of removal of coarse woody debris, past landscape) were not recorded in a sufficiently standard way to be used as covariates in dead wood models. Similarly, plot-level living tree density or above ground biomass (expressed in kg.ha⁻¹) of standing living trees, presumably surveyed in subplot 2, were not available.

A.2.2 BioSoil database and dead wood protocole

In the framework of the large collaborative European Forest Focus BioSoil-Biodiversity project, a system of circular concentric subplots was built around ICP level I plots to collect additional data on stand structure and biodiversity in the field between 2005 and 2008. The selection of the ICP level I plots to be included in the BioSoil Forest Biodiversity project in the period of 2005–2008 was carried out by the countries (Galluzzi et al., 2019). Overall a total of geocoded 3,243 Level I plots were considered with their associated spatial coordinates and general information, and includes 19 European Countries (Puletti et al., 2017): Austria, Belgium (only Flanders region), Cyprus, Czech Republic, Denmark, Finland, France, Germany with eight federal states, Hungary, Ireland, Italy, Latvia, Lithuania, Poland, Slovakia, Slovenia, Spain, Sweden, United Kingdom. BioSoil project results in the ICP Forests LI-BioDiv database, a multi-dimensional forest geodatabase that contains raw data of forest structure and vegetation records to calculate simple plot-level structural and compositional forest variables (biomass, dead wood volume, alpha diversity; Bastrup-Birk et al., 2007; Hiederer and Durant, 2010).

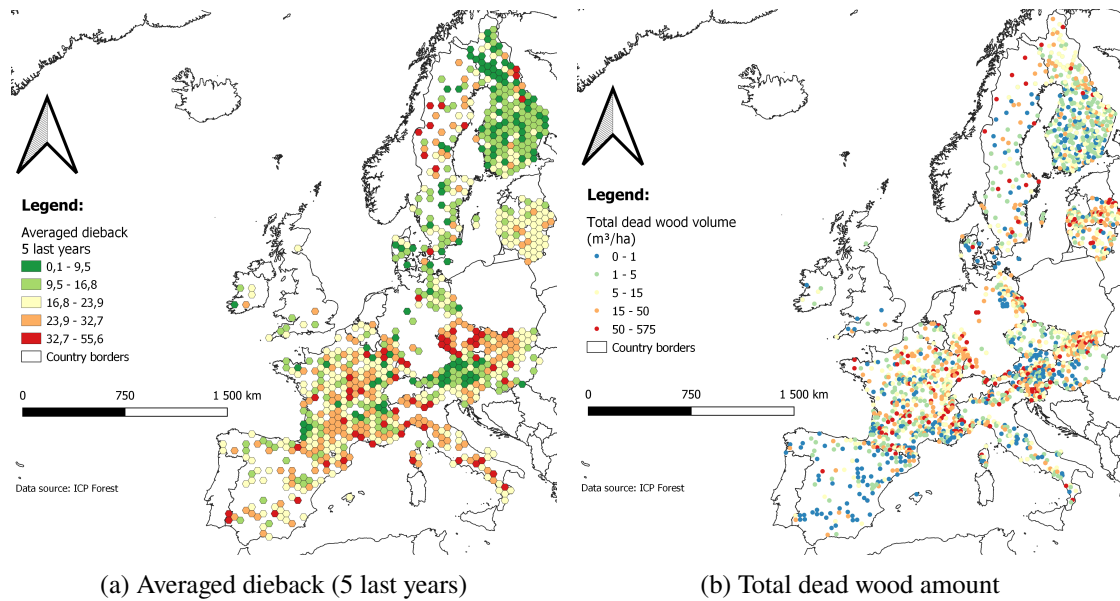


Figure S3.1 – Overview of selected plots for cross-analysis of European ICP-defoliation (left) and Biosoil-dead wood data sets (right).

Dead wood was assessed over an area of 400 m² (BioSoil subplots 1 and 2, radius of 11.28 m; [Puletti et al., 2017](#)). Coarse woody debris (incl. lying dead trees), snags and stumps, more than 10 cm in diameter, were measured. Only snags and stumps more than 130 cm in height were considered. All standing dead trees were treated as snags. Diameter, length or height, species type and decay class were recorded for each dead wood piece. Raw data were processed by [Puletti et al. \(2017; 2019\)](#) to provide pan-European variables describing the volume of all dead wood and the volume of several dead wood types. In our study, we considered the following response variables: (i) volume of all dead wood, (ii) volume of fresh dead wood (i.e. the addition of "Vm3_dec1_Biosoil" and "Vm3_dec2_Biosoil"), (iii) volume of decayed dead wood (i.e. the addition of "Vm3_dec4_Biosoil" and "Vm3_dec5_Biosoil"), (iv) volume of standing dead wood (i.e. the addition of standing dead trees and snags), (v) volume of ground-lying dead wood (i.e. the addition of lying dead trees and coarse woody debris).

A few environmental covariates were collected from Biosoil data: (i) management intensity (grouped into 2 classes: "recently.harvested", i.e. with management evidence within the last 10 years, and "no.recent.harvest", i.e. unmanaged (no management evidence) or managed a longer time ago (management evidence but for more than 10 years ago)), (ii) average stand age (grouped into 3 classes: "mature" [>100 yrs], "midaged" [41-100 yrs], "young" [1-40 yrs]), (iii) elevation (a.s.l.), a continuous quantitative variable, (iv) genus of the dominant tree species, (v) group of the dominant tree species: coniferous, deciduous and mixed.

A.2.3 Database joining: plot matching in time series

After a harmonization step of plot names and coordinates in both data sets (ICP-defoliation and Biosoil-dead wood), only plots with matched data in both data sets were selected. Plots with a discontinuity of only 1 year on the chronicle were retained, with the missing value reconstructed from contiguous years. Plots with defoliation measurement discontinuities greater than 2 years were deleted. Biosoil-ICP plot matching around the longitudinal measurements of defoliation from 1989 to 2007, finally provided 2070 5-year time series, 1804 10-year chronicles and 1399 15-year data sets. This approach allowed the selection of 10-year chronicles (i.e. 1995-2005, 1996-2006, 1997-2007) in 17 countries, from 5 plots in Ireland and 9 plots in the United Kingdom, to 337 plots in Finland and 461 plots in France.

A.2.4 Calculation of synthetic dieback metrics

Sixteen univariate metrics, summarizing changes in defoliation throughout the 10-year period prior to the Biosoil dead wood measurements, were calculated (Tab. S3.1). Some parameters describe the potential immediate effects of the severity of defoliation in a given year in the near past: (i) defoliation level of the previous year ("n-1"), (ii) defoliation level of the previous year before last ("n-2"), (iii) defoliation level of the year before the previous year before last ("n-3"). Other dieback metrics relate to cumulative effects of dieback levels in the near or the distant past; (i) Average dieback level over the last 2 years ("last2"), (ii) Average dieback level over the last 3 years ("last3"), (iii) Average dieback level over the last 5 years ("last5"), (iv) Average dieback level over the first 5 years of the 10-year chronicle ("first5"), (v) time elapsed since peak dieback ("time.peak"). Several measures of dieback depict general trends in the level of defoliation over the 10-year chronicle, such as cumulative metrics: (i) arithmetic mean of annual defoliation level ("arimean"), (ii) geometric mean of annual defoliation level ("geomean"), (iii) Area Under the defoliation-time Curve ("AUC"), i.e. the cumulative sum of defoliation, and an overall trend metric: (iv) slope estimate of the linear regression line of dieback level versus time ("slope"). Finally, some metrics are associated with defoliation severity and repetition over the 10-year chronicle, and potentially time-lagged effects: (i) maximum dieback level ("maxi"), (ii) total number of years spent beyond the peak level, successive or not ("years.peak"), number of peaks, consecutive or discontinuous, i.e. number of severe defoliation events, i.e. defoliation frequency ("nb.peaks"), duration of the longest peak, i.e. longest cumulative continuous time during which the level of defoliation was greater than the peak value ("lgst.peak"; Tab. S3.1).

A peak in dieback was defined as a year in which the level of defoliation exceeded a relative threshold, i.e. the third quartile value. In our 10-year chronicle data, peak value was 25%. The defoliation level was greater than 25% throughout the whole 10-year chronicle in 8% of the plots, and lower than 25% throughout the whole 10-year chronicle in 48% of the plots. On average, (i) the level of defoliation exceeded the 25% threshold value around 2.5 years, and (ii) the maximum value per chronicle reaches 27%.

Table S3.1 – Overview of response dead wood variables, dieback predictors and environmental covariates in the 10-year chronicle dataset.

Variable	Description	Range (min-max)	Mean ± se
Response dead wood variables			
vol_bm	Volume of all dead wood pieces (m ³ .ha ⁻¹)	0.00 - 574.45	17.86 ± 0.87
vol_bmf	Volume of fresh dead wood (decay class 1 or 2 from the Biosoil protocol) (m ³ .ha ⁻¹)	0.00 - 342.42	7.94 ± 0.53
vol_bmc	Volume of decayed dead wood (decay class 4 or 5 from the Biosoil protocol) (m ³ .ha ⁻¹)	0.00 - 291.46	5.03 ± 0.32
vol_bmd	Volume of standing dead wood (standing dead trees + snags) (m ³ .ha ⁻¹)	0.00 - 555.74	7.36 ± 0.62
vol_bms	Volume of ground-lying dead wood (lying dead trees + coarse woody debris, excluding Fine Woody Debris less than 10cm in diameter) (m ³ .ha ⁻¹)	0.00 - 307.11	8.15 ± 0.50
Dieback parameters			
n-1	Defoliation level of the previous year	0 - 100	20.61
n-2	Defoliation level of the previous year before last	0 - 100	20.20
n-3	Defoliation level of the year before the previous year before last	0 - 100	19.66
last2	Average dieback level over the last 2 years	0 - 78.13	20.40
last3	Average dieback level over the last 3 years	0 - 80	20.16
last5	Average dieback level over the last 5 years	0.08 - 69.25	19.50
first5	Average dieback level over the first 5 years of the 10-year chronicle	0 - 61.56	17.56
time.peak	Time elapsed since last peak dieback	0 - 16	7.95
arimean	Arithmetic mean of annual defoliation level	0.05 - 57.99	18.72
geomean	Geometric mean of annual defoliation level	0 - 56.88	17.82
AUC	Area Under The Curve	0.05 - 51.73	16.98
slope	Slope estimate of the linear regression line of dieback level versus time	-2.94 - 5.11	0.37
maxi	Maximum dieback level	0.42 - 100	27.73
years.peak	Total number of years spent beyond the peak level	0 - 11	2.93
nb.peaks	Number of peaks	0 - 4	0.88
lgst.peak	Duration of the longest peak	0 - 11	2.46
Environmental covariates			
Management intensity	recently.harvested, i.e. with management evidence within the last 10 years	1017 plots	
	no.recent.harvest, i.e. unmanaged (no management evidence) or managed a longer time ago (management evidence but for more than 10 years ago)	707 plots	
Average stand age	Mature (>100 yrs)	379 plots	
	Midaged (41-100 yrs)	1059 plots	
	Young (1-40 yrs)	315 plots	
	Irregular	43 plots	
Elevation	a.s.l. in meters, continuous quantitative	0 - 2489	438.38 ± 0.23
Dominant tree species	Genus	<i>Quercus</i> (332 plots), <i>Fagus</i> (180 plots), <i>Betula</i> (71 plots), Other deciduous (151 plots), <i>Pinus</i> (574 plots), <i>Picea</i> (408 plots), Other coniferous (88 plots)	
	Group	Coniferous (947 plots), Deciduous (656 plots), Mixed (201 plots)	

A.2.5 Modelling strategy

Data analysis was conducted with R software 4.1.2. (R Core Team, 2022). We assessed the relative effect on dead wood of (i) metrics depicting defoliation dynamics, (ii) topographic variables (i.e. el-

evation); (ii) forest type (dominating tree species); (iii) other environmental covariates related to forest management (stand age, management intensity, etc.); and (v) interactions between all of the independent variables explored (Tab. S3.1).

We tested the effect of these predictors on each of the five dead wood response variables using generalized linear mixed model (GLMM), including the Biosoil year and the country as random variables on the intercept. Dead wood response variables included a high number of "0" values: 11% for the volume of all dead wood, 33% for fresh dead wood, 31% for decayed dead wood, 60% for standing dead wood, 37% for ground-lying dead wood. We looked for a family of distributions to better fit the distribution of dead wood response variables, non discrete positive variables, non-Gaussian, zero-inflated data, and a continuous distribution of positive values. Due to the linear link between log-variance and log-mean of random draws of 100 samples in response variable, we chose the Tweedie distribution from the class of compound Poisson–gamma (with log as link function). We used `glmmTMB` function of the `glmmTMB` R-package (Magnusson et al., 2020). We tested the accuracy of chosen distribution using the residual diagnostic method from the DHARMA R-package (Hartig and Lohse, 2022). We handled over-dispersion in residues by adding the plot level in random effects. We also added a structure of spatial autocorrelation decaying exponentially with distance between plots to describe spatial dependency among plots in the sampling design.

Fixed effects (dieback parameters and environmental covariates) were alternatively included in univariate models, and sequentially included in multiplicative models considering interactions (`dredge` function) and taking between-predictor collinearity into account. For each given response variable, best models were identified using model comparison by both AIC and BIC criteria.

For each response variable and for most influencing variables, we not only analyzed the significance, but also the magnitude of the effect (Gosselin et al., 2017b). We simulated an increase in the numeric explanatory dieback variable and studied the magnitude of the consecutive change in the mean of the response dead wood variable. The simulated increase was chosen as the standard deviation of the variable. We considered the magnitude of the effect negligible (even if statistically significant) if the variation ΔX of the explanatory variable X led to a variation in the mean of the response variable that was less than 10% of the mean of the response variable's initial value. This resulted in a 10,000-sample distribution of the relative increase in the response variable under consideration from which we extracted the mean and the 99% confident interval.

A.3 Results

A.3.1 Best single- and multiple-variable models explaining dead wood volumes: most influential covariates of dieback and/or environment

Of the synthetic parameters describing the dynamics of tree decline over the 10-year period prior to the dead wood measurements, only two had significant effects on dead wood volumes: the average level of dieback over the last five years (`last5`) and the time elapsed since peak dieback (i.e. *time.peak*; Tab. S3.1). We did not observe any significant relationship between dead wood and dieback parameters describing the severity of defoliation in the very recent past, or the average level of decline in the mid-ancient past (from 5 and 10 years before), or maximum level of decline or overall sums, averages or trends in defoliation or defoliation frequency over the previous 10-year period.

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Table S3.2 – Generalized Linear Mixed modelling (Tweedie fitting) of the defoliation-dead wood relationship. Null models include selected random effect and exponential spatial covariance structure. Selection criteria of models were AIC and BIC.

Model	Predictors	Models	AIC	BIC	Estimates ± SE of die-back effects		
Total dead wood volume							
Null model			13,237	13,276			
Single-variable models	Dieback variables	~last5	13,205	13,249			
		~time.peak	13,212	13,256			
		~age	13,198	13,258			
	Environmental covariables	~altitude	13,236	13,280			
		~tree.genus	13,226	13,298			
		~tree.group	13,248	13,298			
Multiple-variable models	Best additive model	~last5 + age + altitude + tree.genus	13,125	13,229			
		~last5 + time.peak + age + altitude + tree.genus + tree.group + age × last5	13,105	13,248	last5: +0.04 ± 0.01; time.peak: -0.02 ± 0.01		
	Best multiplicative model						
Standing dead wood volume							
Null model			7,589	7,617			
Single-variable models	Dieback variables	~last5	7,537	7,581	last5: +0.05 ± 0.01		
	Environmental covariables	no significant environmental effect					
Multiple-variable models	Best additive model	no better multi-variable additive model					
	Best multiplicative model	no better multi-variable multiplicative model					
Lying dead wood volume							
Null model			9,808	9,836			
Single-variable models	Dieback variables	~time.peak	9,727	9,771			
		~age	9,705	9,765			
		~altitude	9,795	9,805			
	Environmental covariables	~tree.genus	9,720	9,792			
		~tree.group	9,734	9,780			
		~management	9,802	9,830			
Multiple-variable models	Best additive model	~time.peak + age + tree.genus + tree.group	9,666	9,775			
	Best multiplicative model	no better multi-variable multiplicative model					
Fresh dead wood volume							
Null model			9,823	9,850			
Single-variable models	Dieback variables	~last5	9,765	9,809			
		~time.peak	9,790	9,825			
		~age	9,809	9,855			
	Environmental covariables	~altitude	9,830	9,861			
		~tree.genus	9,823	9,851			
		~tree.group	9,835	9,870			
		~management	9,841	9,885			
		Multiple-variable models	Best additive model	~last5 + time.peak + age + tree.genus	9,761	9,815	
			Best multiplicative model	~last5 + time.peak + age + tree.genus + age × last5 + tree.genus × last5	9,755	9,805	last5: +0.07 ± 0.04; time.peak: -0.03 ± 0.01
Decayed dead wood volume							
Null model			8,565	8,604			
Single-variable models	Dieback variables	no significant dieback effect					
		~age	8,531	8,591			
		~altitude	8,538	8,582			
	Environmental covariables	~tree.genus	8,549	8,621			
		~tree.group	8,566	8,615			
		~management	8,566	8,615			
Multiple-variable models	Best additive model	~age + altitude + tree.genus	8,515	8,580			
	Best multiplicative model	no better multi-variable multiplicative model					

Last5 was the most leading predictor of the volume of all dead wood, but its effect was weaker than the effect of stand age. The second most influencing dieback variable was *time.peak*, and was more determining than all environmental variables except stand age. The best multi-variable model explaining the volume of all dead wood included *last5*, *time.peak* and stand age, but also elevation, tree genus and tree group as well as the interaction between *last5* and stand age.

Last5 was also the most influential variable on fresh dead wood volume, and had a stronger positive effect than general environmental variables, such as stand age, management intensity or tree group. The second key dieback variable explaining dead wood was *time.peak*, which also had a stronger negative effect than the other environmental variables. The best multi-variable model included *last5* and *time.peak*, as well as stand age, tree genus and interactions between *last5* and tree genus, and between stand age and *last5*.

Last5 was the only dieback variable controlling the volume of standing dead wood. The higher the average level of dieback over the past five years, the greater the volume of standing dead wood on the plot. The best multiple-variable model explaining the volume of lying dead wood included stand age, tree genus, tree group as well as *time.peak*. Stand age and tree genus had the strongest individual effects on lying dead wood volume, followed by *time.peak* and tree group. The longer the time lag between the last dieback peak and the dead wood measurement, i.e., the older the dieback peak, the lower the volume of dead wood lying in the plot.

The volume of decayed dead wood was not significantly affected by any of the measures describing dieback dynamics over the previous 10-year period, but it was influenced by stand age, elevation and tree genus, all included in the best multi-variable model.

Management intensity was never implicated in the best models explaining dead wood. Overall, standing dead wood or fresh dead wood volumes were best explained by dieback metrics, while total, lying, or decayed dead wood volume was best determined by environmental parameters.

A.3.2 Magnitude of dieback effects implied in the best models

Across all European plots, the volume of total dead wood, fresh dead wood, or standing dead wood was on average 33% (21-47% IC99%), 54% (33-76% IC99%) and 66% (40-96% IC99%), respectively, higher when the average level of dieback over the past five years was increased by 10 (Fig. S3.2, Tabs. S3.3, S3.4 and S3.5). Local volume of all dead wood, volume of fresh dead wood, and volume of standing dead wood were doubled when the average level of dieback over the past 5 years was increased by 24, by 17 and by 14, respectively (Fig. S3.2). Local volume of all dead wood, or dead wood lying, or fresh dead wood was on average 27% (16-39% IC99%), 21% (7-37% IC99%) or 41% (24-60% IC99%) lower, respectively, when the time elapsed since peak dieback was increased by 7 years (Fig. S3.2, Tabs. S3.3, S3.4 and S3.5).

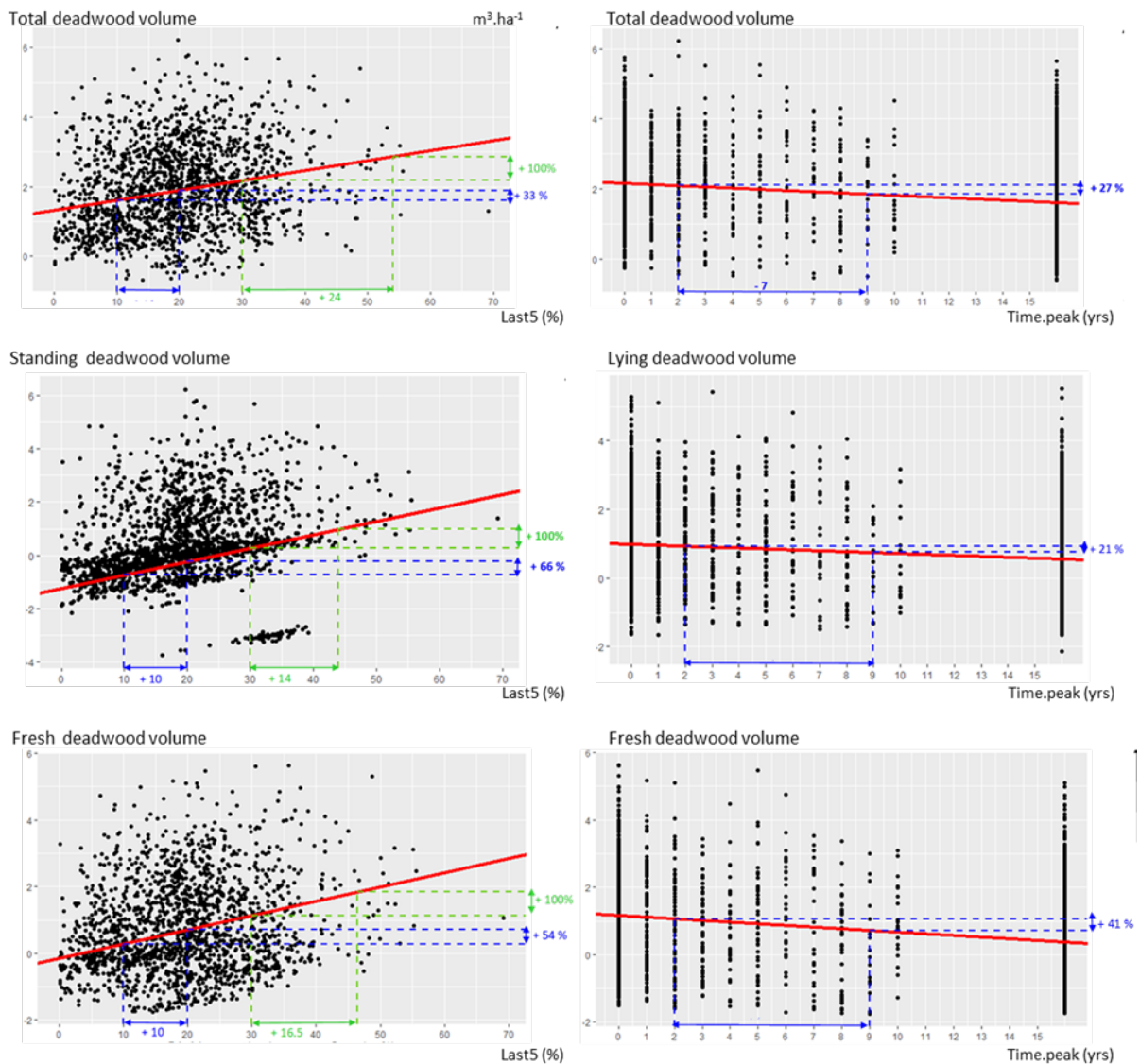


Figure S3.2– Magnitude from models of the effect of forest dieback level on dead wood volumes, calculated as the increase or decrease in the response variable to a 10% increase in the average level of dieback in the last 5 years (i.e. observed standard deviation of Last5), when the time elapsed since peak dieback was increased by 7 years (i.e. observed standard deviation of Time.peak). dead wood volumes on Y-axis are in log values.

A.3.3 Variation in the effects of dieback on dead wood volumes in subsets of data based on forest context variables

The positive effect of dieback parameters (*last5*) on dead wood volumes was significant in all tree groups (deciduous-, conifer-dominated, mixed) for all, fresh and standing dead wood (except in mixed forests for the non-testable standing dead wood; Tabs. S3.3, S3.4 and S3.5). It was stronger in coniferous than in deciduous forests, for all and standing dead wood, with mixed forests in between. The effect of the *time.peak* metric on dead wood was significant in all tree groups for all dead wood, but not in deciduous forests for ground-lying and fresh dead wood. The CIs associated with the magnitude values actually overlapped between tree groups (Tabs. S3.3, S3.4 and S3.5).

Consistent with the significant interaction between *last5* and tree genus in the best multiple-variable model for fresh dead wood (Tab. S3.2), the dieback-dead wood relationship actually varied with dominant tree species. The dieback parameters (*last5* and *time.peak*) had a significant effect on total and fresh dead wood in oak, pine and spruce forests, but not in birch and beech forests, which were also less represented in the data set (Tabs. S3.2, S3.3 and S3.4). Similarly, the effect of the *time.peak* metric on ground-lying dead wood was significant in oak, pine and spruce forests, but not in birch and beech forests (Tab. S3.5). *Last5* was a significant dieback variable controlling standing dead wood volume in pine and spruce forests only (Tab. S3.5). Overall, the magnitudes of effects were stronger in oak forests, than in spruce and then pine forests, but the CIs of the values overlapped.

Consistent with the significant interaction between *last5* and stand age for all dead wood and fresh dead wood, stand age class affected the significance and strength of several dieback-dead wood relationships. The relationship between dieback parameters (*last5* and *time.peak*) and total dead wood was stronger in young stands than in middle-aged stands, and not significant in mature stands (Tab. S3.2). Dieback metrics (*last5* and *time.peak*) and fresh dead wood were correlated in mature and middle-aged stands, while the models based on data from the young age class did not converge (Tab. S3.3). The dieback metric (*time.peak*) was not related to lying dead wood for any of the stand age classes (Tab. S3.4), while standing dead wood was affected by dieback (*last5*) in middle-aged stands only (Tab. S3.5).

The relationship between dieback and dead wood was significant in each of the management intensity classes for each dead wood category. Although it should be noted that magnitude CI values overlapped between classes, the relationship tended to be stronger in recently logged stands than in unharvested stands for all and fresh dead wood. In contrast, it tended to be stronger in unharvested than in recently logged stands for standing and lying dead wood. The dieback-dead wood relationship was significant in lowland forests for all dead wood, fresh dead wood, standing dead wood and lying dead wood, and in highland forests for all dead wood and fresh dead wood, but never significant at intermediate elevations.

Table S3.3 – Significance and magnitude of dieback effects on total dead wood volume in every subset (full data in Suppl. Mat.). Magnitude was calculated as the increase or decrease in the response variable to a 10% increase in the average level of dieback in the last 5 years (i.e. observed standard deviation of *Last5*), or to a 7-year increase of the last peak of dieback (i.e. observed standard deviation of *Time.peak*).

Variable	Type	Plot number	null model	Last5		Time.peak	
			AIC	AIC	Magnitude (CI 99%)	AIC	Magnitude (CI 99%)
Tree.genus	<i>Quercus</i>	332	2,192	2,174**	+68% (29%; 116%)	2,172**	-83% (-35%; -142%)
	<i>Fagus</i>	180	1,483	1,484 ^{ns}		1,485 ^{ns}	
	<i>Betula</i>	71	527	529 ^{ns}		529 ^{ns}	
	<i>Pinus</i>	574	3,989	3,976**	+43% (16%; 75%)	3,970**	-40% (-18%; -64%)
	<i>Picea</i>	408	3,054	3,023**	+62% (33%; 95%)	3,032**	-50% (-23%; -72%)
Age	<i>Mature</i>	379	3,024	3,025 ^{ns}		3,024 ^{ns}	
	<i>Midaged</i>	1,059	7,858	7,853*	+18% (2%; 37%)	7,846**	-22% (-8%; -38%)
	<i>Young</i>	315	1,961	1,947**	+50% (19%; 89%)	1,957**	-34% (-2%; -72%)
Management	<i>recently.harvested</i>	1,017	7,906	7,581**	+37% (20%; 56%)	7,592**	-25% (-11%; -40%)
	<i>no.recent.harvest</i>	707	5,052	5,042**	+26% (8%; 47%)	5,043*	-25% (-7%; -44%)
Tree.group	<i>Deciduous</i>	656	4,858	4,854*	+20% (1%; 43%)	4,854*	-19% (-1%; -41%)
	<i>Mixed</i>	201	1,536	1,530*	+45% (6%; 95%)	1,533*	-27% (-2%; -63%)
	<i>Coniferous</i>	947	6,870	6,830**	+46% (28%; 67%)	6,838**	-37% (-21%; -55%)
Altitude	<i>Lowland</i>	980	6,991	6,941**	+54% (34%; 77%)	6,955**	-37% (-22%; -54%)
	<i>Hilly</i>	354	2,660	2,659 ^{ns}		2,658*	-21% (4%; -51%)
	<i>Highland</i>	470	3,597	3,592*	+27% (3%; 56%)	3,595*	-19% (2%; -43%)

** = $\Delta AIC > 10$, * = $\Delta AIC < 10$, ns = $\Delta AIC < 2$ or AIC lower for the null model

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Table S3.4 – Significance and magnitude of dieback effects on volume of fresh dead wood in every subset (full data in Suppl. Mat.). Magnitude was calculated as the increase or decrease in the response variable to a 10% increase in the average level of dieback in the last 5 years (i.e. observed standard deviation of Last5), or to a 7-year increase of the last peak of dieback (i.e. observed standard deviation of Time.peak).

Variable	Type	Plot number	null model	Last5		Time.peak	
			AIC	AIC	Magnitude (CI 99%)	AIC	Magnitude (CI 99%)
Tree.genus	<i>Quercus</i>	332	1,394	1,379**	+109% (39%; 205%)	1,385*	-105% (-25%; -223%)
	<i>Fagus</i>	180	1,019	1,020 ^{ns}		1,021 ^{ns}	
	<i>Betula</i>	71	463	464 ^{ns}		464 ^{ns}	
	<i>Pinus</i>	574	3,151	3,139**	+59% (19%; 110%)	3,136**	-51% (-19%; -88%)
	<i>Picea</i>	408	2,406	2,381**	+66% (30%; 112%)	2,383**	-64% (-28%; -107%)
Age	<i>Mature</i>	379	2,254	2,248*	+47% (7%; 98%)	2,246*	-50% (-12%; -98%)
	<i>Midaged</i>	1,059	5,897	5,886**	+37% (12%; 66%)	5,884**	-33% (-12%; -57%)
	<i>Young</i>	315	1,405	NA		NA	
Management	<i>recently.harvested</i>	1,017	5,594	5,566**	+60% (32%; 94%)	5,573**	-44% (-20%; -70%)
	<i>no.recent.harvest</i>	707	3,785	3,771**	+45% (17%; 79%)	3,778*	-32% (-7%; -62%)
Tree.group	<i>Deciduous</i>	656	3,336	3,328*	+44% (11%; 85%)	3,335 ^{ns}	
	<i>Mixed</i>	201	1,176	1,173*	+61% (2%; 147%)	1,168*	-67% (-15%; -134%)
	<i>Coniferous</i>	947	5,307	5,274**	+61% (33%; 95%)	5,275**	-53% (-28%; -80%)
Altitude	<i>Lowland</i>	980	5,524	5,476**	+81% (49%; 119%)	5,493**	-51% (-28%; -78%)
	<i>Hilly</i>	354	1,838	1,839 ^{ns}		1,840 ^{ns}	
	<i>Highland</i>	470	2,465	2,455**	+56% (16%; 106%)	2,455*	-52% (15%; -99%)

** = $\Delta AIC > 10$, * = $\Delta AIC < 10$, ns = $\Delta AIC < 2$ or AIC lower for the null model

Table S3.5 – Significance and magnitude of dieback effects on total dead wood volume in every subset (full data in Suppl. Mat.). Magnitude was calculated as the increase or decrease in the response variable to a 10% increase in the average level of dieback in the last 5 years (i.e. observed standard deviation of Last5), or to a 7-year increase of the last peak of dieback (i.e. observed standard deviation of Time.peak).

Variable	Type	Plot number	Standing dead wood			Ground-lying dead wood		
			null model	Last5		null model	Time.peak	
			BIC	BIC	Magnitude (CI 99%)	AIC	AIC	Magnitude (CI 99%)
Tree.genus	<i>Quercus</i>	332	1,402	NA		1,460	1,457*	-61% (-1%; -151%)
	<i>Fagus</i>	180	788	793 ^{ns}		1,141	1,143 ^{ns}	
	<i>Betula</i>	71	359	363 ^{ns}		423	425 ^{ns}	
	<i>Pinus</i>	574	2,350	2,334**	+103% (41%; 186%)	2,923	2,915*	-34% (-7%; -66%)
	<i>Picea</i>	408	1,561	1,544**	+126% (52%; 228%)	2,317	2,306**	-52% (-17%; -96%)
Age	<i>Mature</i>	379	1,718	1,722 ^{ns}		2,343	2,343 ^{ns}	
	<i>Midaged</i>	1,059	4,693	4,674**	+70% (33%; 117%)	5,755	5,754 ^{ns}	
	<i>Young</i>	315	1,026	NA		1,345	1,346 ^{ns}	
Management	<i>recently.harvested</i>	1,017	4,103	4,096*	+50% (16%; 92%)	5,741	5,739*	-15% (2%; -35%)
	<i>no.recent.harvest</i>	707	3,223	3,199**	+76% (38%; 124%)	3,561	3,557*	-26% (-2%; -55%)
Tree.group	<i>Deciduous</i>	656	2,976	2,971*	+48% (13%; 92%)	3,488	3,490 ^{ns}	
	<i>Mixed</i>	201	NA	NA		1,183	1,178*	-50% (-5%; -109%)
	<i>Coniferous</i>	947	3,780	3,743**	+100% (55%; 156%)	5,095	5,082**	-31% (-11%; -54%)
Altitude	<i>Lowland</i>	980	3,990	3,941**	+125% (75%; 188%)	5,118	5,105**	-33% (-12%; -57%)
	<i>Hilly</i>	354	1,538	1,541 ^{ns}		2,033	2,035 ^{ns}	
	<i>Highland</i>	470	NA	NA		2,629	2,630 ^{ns}	

** = ΔAIC or $BIC > 10$, * = ΔAIC or $BIC < 10$, ns = ΔAIC or $BIC < 2$ or AIC or BIC lower for the null model

A.4 Discussion

We here confirmed significant effects of dieback on dead wood stocks, compared with other environmental variables. Plot-level volumes of dead wood correlated to near past levels of local dieback. From our results, the average level of dieback in the last 5 years and the age of a possible dieback peak are more important for the structure of the dead wood stock than (i) the very recent level of dieback, (ii) older levels of dieback, (iii) the intensity of extreme past diebacks or the frequency of past dieback peaks in the last 10 years, and (iv) the average or cumulative dieback in the last 10 years.

Across European forests, the dead wood-dieback relationship strongly varied with forest context. The positive effects of dieback on dead wood were stronger on fresh than on decayed dead wood, which would probably require longer time-series. They were stronger in recently-managed than in unmanaged plots, in young than in mature plots and in coniferous than in deciduous plots.

Similarly, Bujoczek and Bujoczek (2022) demonstrated that the extent of damage to living trees by pathological symptoms adversely affecting their health was one of the main significant factors influencing dead wood stocks throughout Polish forests. Dead wood volume may be affected by the temporarily increased mortality of a given declining species, as in the case of ash and spruce stands. In line with our results, they also identified stronger relationships in managed forests than in nature reserves.

Although we have demonstrated significant relationships between dead wood and synthetic variables summarizing the 10-year chronicle into single variables here, it may be instructive to explore whether dead wood stocks depend on past diebacks in a more complex way. It would require to find a way to treat the entire time series of longitudinal predictors, to manage variations in stationarity of time series, to handle with autoregressive processes in the defoliation chronicle (Bull et al., 2020).






A.5 Conclusion

Our study illustrates the interest of large-scale forest database cross-analyses. Other data from the Biosoil LI-BioDiv database could be valued (canopy closure, number of tree layers, alpha diversity of vascular plant species, referred to ICP subplot 2) for other research purposes aimed at studying cross-relationships between multiple forest variables. The mapping of some disturbance parameters (year of last disturbance, disturbance intensity) in European forests from 1986 to 2008 by interpretation of Landsat data, at a spatial resolution of 500m (Senf and Seidl, 2021a) is another source of disturbance data at the European forest scale which could improve our modelling of disturbance-decline-dead wood relationships.

A.6 Acknowledgements

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Trait-based response of dead wood and tree-related micro-habitats to dieback in temperate forests

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Abstract

Deadwood and tree-related microhabitats (TreMs) are affected by forest management and are therefore relatively rare in managed European forests. Senescence and tree mortality resulting from forest dieback should provide these habitats. However, these contributions are expected to be highly context-dependent (e.g. due to tree species or type of disturbance affecting tree vitality).

We used study plots established along a gradient of forest dieback in two distinct contexts: fir-dominated forests (*Abies alba*) in the French Pyrenean mountains, and oak-dominated forests (*Quercus* spp.) in the Loire valley, in the lowlands. Dieback in both contexts was mainly triggered by successive drought events. In these study plots we recorded living and dead trees using a relascope protocol. We recorded the species, diameter and decomposition in case of dead wood. Finally, we listed the TreMs present on each tree.

We shown that forest dieback influences both dead wood and TreMs profiles. The amount of dead wood generally and significantly increased due to dieback. Similarly, tree injury and saproxylic fungi were positively affected by dieback. We showed that changes in TreMs profiles were due to changes in deadwood profiles.

Forest dieback increased the amount of dead wood and changed the profiles of the TreMs so that the habitats generated are closer to those associated with old growth forests.

Keywords: Forest dieback; Dead wood; Tree-related microhabitats; Disturbance legacy; Forest management

Résumé

Le bois mort et les dendromicrohabitats (TreMs) sont affectés par la gestion forestière et sont donc relativement rares dans les forêts européennes gérées. La sénescence et la mortalité des arbres résultant du dépérissement de la forêt devraient fournir ces habitats. Néanmoins, ces contributions devraient être fortement dépendantes du contexte (par exemple, en raison de l'espèce d'arbre ou du type de perturbation affectant la vitalité de l'arbre).

Nous avons utilisé des placettes d'étude établies le long d'un gradient de dépérissement forestier dans deux contextes distincts : des forêts à dominante de sapins (*Abies alba*) dans les montagnes pyrénéennes françaises, et des forêts à dominante de chênes (*Quercus* spp.) dans la vallée de la Loire, en plaine. Le dépérissement dans les deux contextes a été principalement déclenché par des événements de sécheresse successifs. Dans ces placettes d'étude, nous avons enregistré les arbres vivants et morts en utilisant un protocole relascopique. Nous avons noté l'espèce, le diamètre et l'état de décomposition en cas de bois mort. Enfin, nous avons listé les TreMs présents sur chacun d'entre-eux.

Nous avons montré que le dépérissement forestier influence à la fois les profils de bois mort et de TreMs. La quantité de bois mort a généralement et significativement augmenté en raison du dépérissement. De même, les blessures des arbres et les champignons saproxyliques ont été positivement affectés par le dépérissement. Nous avons montré que les changements dans les profils de TreMs étaient dus aux changements des profils de bois mort.

Le dépérissement forestier a augmenté la quantité de bois mort et a modifié les profils des TreMs de sorte que les habitats engendrés se rapprochent de ceux liés aux vieilles forêts.

Mots-clés : Dépérissement forestier; Bois mort; Dendromicrohabitats; Héritages de perturbation; Gestion forestière

B.1 Introduction

Disturbance size, frequency and severity have increased across Europe in recent decades, as a result of recent changes in land use and climate (Schelhaas et al., 2003; Seidl et al., 2011, 2014b), such as frequent and persistent periods of anomalous drought (Hari et al., 2020). An increase in natural disturbances, known to shape the structure and dynamics of forest ecosystems, should result in changes in forest cover, structure, and composition (Seidl et al., 2011; Turner, 2010). Natural disturbances indeed generate spatial structural heterogeneity, from the scale of individual trees to landscapes (Seidl et al., 2014a).

Much of our knowledge about natural dynamics in temperate forests is based on observational studies in old-growth remnants that have emphasized small-scale gap dynamics. Relatively little attention has been given to the role of disturbance events on stand structure and composition (Nagel et al., 2014). Yet, disturbances enhance structural heterogeneity of forests by allowing transient accumulations of microhabitats and resources, which may be scarce in managed forest ecosystems (Kulakowski et al., 2017; Meigs et al., 2017; Sallé et al., 2021; Schoennagel et al., 2008). The role of crown dieback events *per se* as mechanisms that create habitat for biodiversity has been rarely recognized (Ojeda et al., 2007), whereas they may be considered as key processes creating habitat, e.g. saproxylic features, over multiple time scales (Fischer et al., 2013). Droughts and windstorms promote the accumulation and diversification of dead wood resources, such as perched dead branches in the canopy, standing killed trees and downed logs (Cours et al., 2021; Swanson et al., 2011; Thorn et al., 2017). Damage to tree health associated to increased canopy openness also favour the formation of certain tree-related microhabitats (TreMs) in damaged trees and in snags (Asbeck et al., 2022; Courbaud et al., 2022; Larrieu et al., 2021; Ojeda et al., 2007). Disturbance events trigger an increase in disturbance legacies but they also cause changes in post-disturbance habitat conditions, such as a decrease in TreMs associated to living trees or in temperature-buffered understorey. Subsequent changes in the availability and distribution of resources in turn affect biotic communities in disturbed forests (Cours et al., 2022; Kozák et al., 2021; Sire et al., 2022).

How the intensity of decline affects patterns of dead wood and TreMs in disturbed forests has been poorly described. Dead wood profile of forest plots, classifying dead wood items based on their size and decay, has been used to describe forest characteristics and to assess forest disturbance history (Christensen et al., 2005; Halme et al., 2019; Stokland, 2001). By extension, variations in dead wood and TreM components in response to disturbance could be analysed using a trait-based approach, i.e. using

a database of eco-morphological traits describing dead wood pieces (Parisi et al., 2018) and tree-related microhabitats.

We had two main objectives. First, we aimed to quantify the consequences of dieback on the quantity (e.g. living tree and dead wood volume, density of cavity-bearing trees, etc.) and diversity of substrates. Could we confirm an accumulation of dead wood substrates and tree-related microhabitats following dieback in two drought-induced dieback case studies in French temperate forests (lowland deciduous forest vs highland conifer forest)? Could we measure an increase in local heterogeneity of stand structure by diversification of dead wood and Trem assemblages? Secondly we hoped to specify whether accumulation patterns for disturbance legacies depend on their ecomorphological traits (e.g. decay stage, saproxylic nature of TreMs, usual position of TreMs on tree, etc.).

B.2 Material and methods

B.2.1 Sampling design

We led our study on two regions designated two different contexts in France: the oak-dominated forests (both *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) in Loire valley (centre of France), and the Silver fir-dominated forests (*Abies alba* Mill.) in French Pyrenees (Fig. 1). In the oak context, we chose 18 plots in two sites of lowland forests: (i) nine plots in the Orleans state forest (107 to 174 m a.s.l.; 48° 00' 28" N 2° 09' 39" E) and (ii) nine plots in the Vierzon state forest (120 to 190 m a.s.l.; 47° 15' 53.9" N 2° 05' 55.4" E). In the Silver fir context (*Abies alba* Mill.), we chose 43 plots in two sites of montane forests: (i) 21 plots in the Aure Valley (Central Pyrenees; 854 to 1570 m a.s.l., 1298 m on average; 42° 51' 46.8" N 0° 36' 08.9" E) and (ii) 22 plots on the Sault Plateau (Eastern Pyrenees; 705 to 1557.3 m a.s.l., 1029 m on average; 42° 50' 58.7" N 2° 00' 41.3" E). All study plots were set up in managed forests, and predominantly surrounded by managed areas. Plots were set up along a forest dieback gradient (Fig. S4.1). In lowland oak context, the main secondary species were Hornbeam (*Carpinus betulus* L.) and Scott pine (*Pinus sylvestris* L.). In montane fir context, the main secondary species were Norway spruce (*Picea abies* (L.) H. Karst) and European beech (*Fagus sylvatica* L.).

B.2.2 Field measurements

Plots were set-up using n° 1 strip (ratio 1/50) of a Bitterlich relascope (Bitterlich, 1984). For each living or dead tree belonging to the plot, we recorded its status (i.e. living, snag, log), tree-species, dbh (minimum dbh to be recorded: 17.5 cm for living trees and logs, 7.5 for snags). Tree-related microhabitats (TreMs) were recorded on living trees and snags, but not on lying dead trees, according to the 47 types described by Larrieu et al. (2018). Each dead wood item (length > 1 m) was measured in length, diameter at mid-length for log and snags <4m, dbh for snags >4m. Mean plot area was about 0.3 ha, depending on the dbh and location of the largest trees. The number of items per hectare was calculated by allocating to every item observed in the relascope sampling the coefficient N_d , in relation to its diameter (d): $N_d = \pi \times 10^8 \times \left(\frac{\arctan(1/50)}{\pi \times dbh} \right)^2$ (Pardé and Bouchon, 1988).

B.2.3 Database of eco-morphological traits for woody elements and tree-related microhabitats (TreMs)

Concerning woody elements, including dead wood pieces and living trees, we directly used field measurements (i.e. position, decay stage (hereafter "saproxylation") and diameter) as eco-morphological traits. We transformed the position into an ordinal scale (i.e. living tree = 3, standing dead wood = 2, lying dead wood = 1) and we directly used wood diameter and the ordinal scale of saproxylation (from 1 = hardwood totally covered by bark, to 4 = very soft wood out of bark).

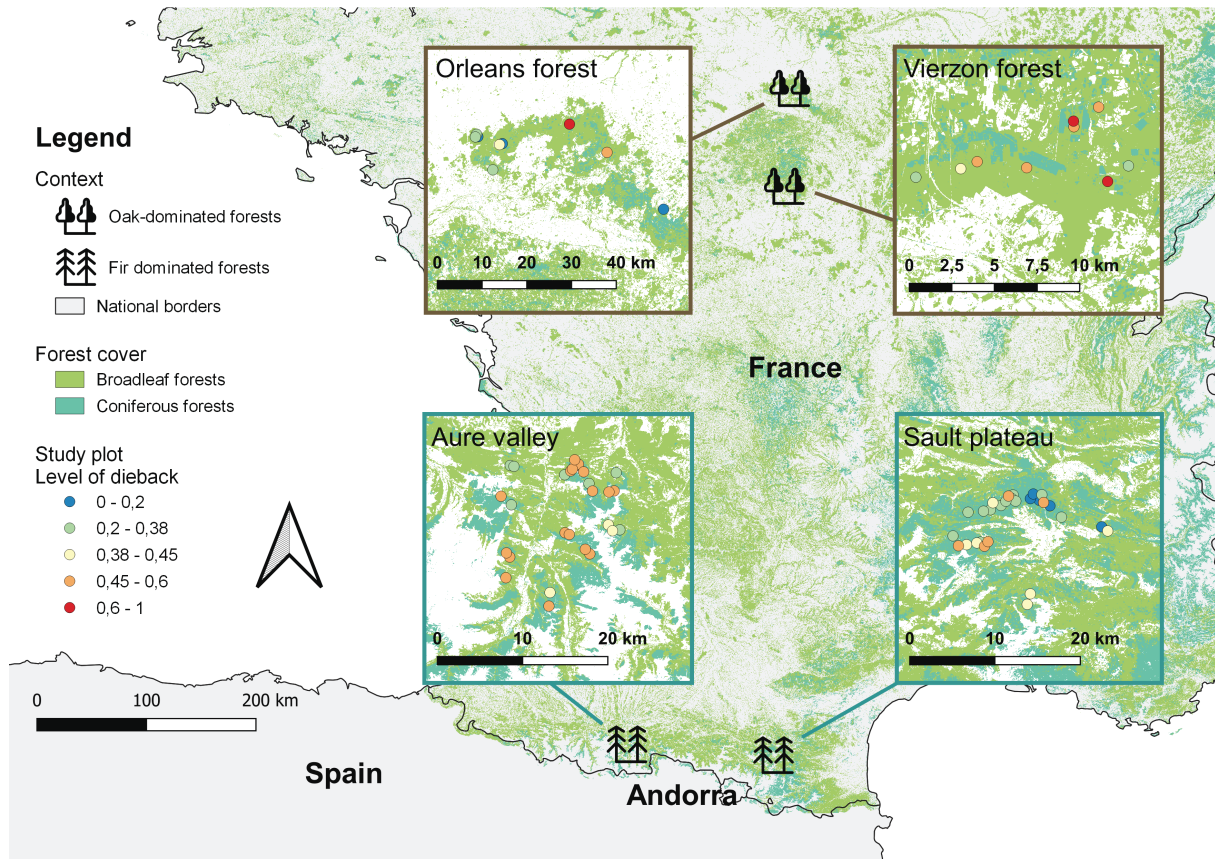


Figure S4.1 – Map of the study plots in each site and of the different contexts.

In addition, we compiled a list of eco-morphological traits for each TreM detected in the field (Tab. S4.1): bearing substrate, position in tree, wetness, life span and ontogenesis. Like Gossner et al. (2013), we allocated each TreM to a category of each trait by a degree of occurrence based on weighting score by expert opinion (L.L.) (0 = no occurrence, 1 = rare occurrence, 2 = common occurrence, 3 = almost systematic occurrence).

B.2.4 Data analysis

Study of dieback effect on woody elements and TreMs using univariate analysis

Data analysis was conducted with R software 4.1.2. (R Core Team, 2022). We conducted our analysis on two substrates of forest ecosystems: (i) woody elements (including dead wood pieces, and sometimes living trees) and (ii) TreMs. When included in woody elements, living trees are mentioned in the legend of figures and tables.

In a first step, we calculated several univariate metrics. We calculated community-weighted means (CWM) and functional dispersion (FDis) for each of the eco-morphological traits using dbFD function of the FD R-package (Tab. S4.1; (Laliberté et al., 2014)). Position and saproxylation traits were characterised for all woody elements (live trees and dead wood pieces), while the diameter trait was noticed for dead wood pieces only. At this stage, we used every tree and piece of dead wood measured in the study plots to calculate CWM and FDis. For the TreMs, we used the associated traits of the 42 types observed in the study plots (Tab. S4.1). We also calculated functional dispersion (FDis) of TreMs (Laliberté et al., 2014). In addition to volume and diversity for woody elements and abundance for each group of TreMs,

we used CWM and FDis for woody elements and TreMs in univariate analysis as response variables. As predictor, we used a standardized index of dieback based on the assessment of the health status of the 20 dominant trees closest to the centre of each plot. The health status was assessed using ARCHI methodology, based on tree architecture (Drénou et al., 2013).

Table S4.1 – Overview of the different eco-morphological traits used in the study for woody elements and TreMs.

Trait group	Trait	Description
Woody elements		
	Position	Status of the tree : 3 = living tree; 2 = snag; 1 = log
	Saproxylation	Decay stage, from 0 = wood on living tree, to 4 = softwood with full absence of bark
	Diameter	Diameter at mid length for logs; diameter and mid-height for snags measuring less than 4m, at breast height otherwise
Tree-related microhabitats		
Substrate	Saproxyllic	TreMs containing dead wood in the process of decay (e.g., rot holes, dead branches)
	Epixylic	TreMs that do not contain dead wood in the process of decay (e.g., bryophytes, lichens, mistletoes)
	Mould	TreMs containing mould (e.g., mainly rot holes)
	Living tree	TreMs mainly borne by living trees (e.g., burrs, epicormic shoots)
	Snag	TreMs mainly borne by snags (e.g., bark pockets and shelters)
	Log	TreMs mainly borne by logs (e.g., rootplates,)
Position	Base	TreMs mainly or strictly occurring at the base of trees (e.g., byophytes, root buttress concavities)
	Trunk	TreMs mainly or strictly occurring on the trunk of trees (e.g., sap runs, trunk rot hole)
	Crown	TreMs mainly or strictly occurring on the crown of trees (e.g., dead tops and branches)
Wetness	Dry	TreMs which are never wet inside since protected from humidity (e.g., , perennial polypores)
	Wet	TreMs often wet when raining (e.g., chimney trunk base rot holes) or intrinsically wet (e.g. active sap run)
Life span	Ephemeral	TreMs maintaining their function for less than a year (e.g., pulpy agarics, slime molds)
	Annual	TreMs maintaining their function about a year (e.g., annual polypores)
	Perennial	TreMs maintaining their function for more than a year (e.g., rot-holes, perennial polypores)
Ontogenesis	Slow	Replacement rate of about decades (e.g., chimney trunk base rot hole, lichens)
	Fairly slow	Replacement rates of about a decade (e.g., rootplates, root buttress concavities)
	Fairly rapid	Replacement rate of less than a decade; e.g., woodpecker breeding cavities, bark losses)
	Rapid	Replacement rate of a year (e.g., slime molds, vertebrate nests)

The standardized dieback index is a value from 0 (i.e. all the 20 trees are healthy), to 1 (i.e. all the 20 trees are dead). We tested the effect of forest dieback on each of univariate metrics using generalized linear mixed model (GLMM), including the site as random variable (i.e. Aure and Sault in fir context, and Orleans and Vierzon in oak context). According to the variable, we used Gaussian (mostly for CWM and FDis metrics), Poisson and negative binomial distribution (mostly for volume, diversity and density of woody elements and TreMs since they are countable and sometime over dispersed response variables). We both used glmmTMB function of the glmmTMB R-package (Magnusson et al., 2020) and mixed_model function of the GLMMadaptive R-package (Rizopoulos, 2022). We tested the accuracy of chosen distribution using the residual diagnostic method from the DHARMA R-package (Hartig and Lohse, 2022). Depending on the response variable, the random variable over-parameterised the model, which did not match any of the available distributions in this case. In this case, we removed the random variable from the model and thus kept it if it finally matched any of the available distributions. If this was not the case, we abandoned the modelling attempt, often due to a lack of data behind the considered variable.

For the successfully modeled response variables, we continue our analysis with the concept of magnitude. The aim here, in addition to significance, was to test the relative amount of difference made by an additional fixed "amount" of dieback, on each of the response variables. To do this, we extracted

each estimate (or β -coefficient) and its standard deviation associated to the standardised forest dieback index for each response variable modeled. Then, we simulated the variation of each estimate coefficient by constructing for each one their Gaussian distribution based on their value and standard deviation. We simulated an increase of 15% of forest dieback (i.e. the standard deviation of forest dieback index in our data set) and modeled their relative contribution for each response variable. This resulted in a 10,000-sample distribution of the relative increase in the response variable under consideration from which we extracted the mean and the 99% confident interval.

Finally, since woody elements are bearing TreMs, we tested the direct and indirect effects of forest dieback on TreMs using structural equations modelling (SEM, or also "confirmatory path analysis"). SEMs allow for the construction of a unique network of multiple predictors and response variables, including at multiple hierarchical levels, where a variable can be both a response variable (y) in a first set of models, and predictor (x) in a second set of models (Lefcheck, 2016). In piecewise SEM, each tested relationship is evaluated individually (Lefcheck, 2016). We simplified models to include only simple linear models in our piecewise SEM. Then we excluded any random effect. In parallel, we added correlated errors that capture relationships between the same set of variables (in our data set, between dead wood variables on the one hand, and between TreMs variables on the other; Lefcheck, 2016). In our piecewise SEM, the final response variables are the TreMs variables and we tested a total of 16 potential relationships. As a result, we added a p.value adjustment and thus removed all effects on TreMs for which the p.value was less than 0.003125 (i.e. $\frac{0.05}{16}$). We validated piecewise SEM using Shipley's test of directed separation, assessing when $P > 0.05$, that there are no missing relationships (Lefcheck, 2016).

Study of dieback effect on woody elements and TreMs compositions using multivariate analysis

In a second step, we implemented a multivariate analysis. First, we generated woody elements species, based on their different characteristics (i.e. combining tree species, position, decay stage and diameter class). Then, we constituted the community matrices: (i) the first using these woody element species, (ii) the second directly using TreMs types (Larrieu et al., 2018). For woody elements, we used the calculated volume per hectare as the abundance variable; for TreMs, we used the density per hectare of bearing trees (note that a tree can bear several TreMs). We then ran distance matrices for woody elements and TreMs in each context, using Bray-Curtis method in the `vegdist` function of the `vegan` R-package (Oksanen et al., 2022). Subsequently, we ran non-metric multidimensional scaling (NMDS) for woody elements and TreMs, using the `metaMDS` R-function (Oksanen et al., 2022). We also implemented PERMANOVA with the "site" effect as a constraint (i.e. in fir context: Aure and Sault, and in oak context: Orleans and Vierzon), to test the effect of forest dieback on woody elements and TreMs compositions (`adonis2` R-function; Oksanen et al., 2022).

In parallel, we divided the standardised forest dieback index into two classes: a low dieback class in which the index does not exceed 0.375, a medium and high dieback class in which index values exceed 0.375 (this value correspond to the separation between low and medium classes when we equally divide the dataset in three classes, i.e. low, medium and high). We extracted β -diversity values within each dieback class (i.e. the "low" and the "mid and high" dieback classes) for woody elements and TreMs through an analysis of similarities (`anosim` R-function; Oksanen et al., 2022). Furthermore, in order to detect the determinant type of woody elements and TreMs in each dieback class and context, we implemented an indicator species analysis without restriction in group combinations, using `multipatt` function of the `indicspecies` R-package (Cáceres et al., 2022). In addition, to test co-variation between woody elements and TreMs matrices (such as searched in the SEM for univariate analysis), we used Procrustes and protest methodology (Oksanen et al., 2022). Finally, to detect any variation of β -diversity between plot in each dieback class, as relative part of the total γ -diversity, we implemented a decomposition of γ -diversity using `adipart` function, in which `Beta.1` represent the β -diversity among plot while `Beta.2` is the β -diversity

among site (Orleans and Vierzon for oak context, and Aure and Sault for fir context) (Oksanen et al., 2022).

B.3 Results

B.3.1 Response of dead wood to dieback level

We measured a significant decrease in living wood volume in fir forests (-26% for a 15% increase in local dieback level), but not in oak forests (Fig. S4.2). At the same time, the level of local dieback had strong positive effects on the volumes of all dead wood (+86% in fir, + 84% in oak), decayed dead wood (+84% in fir, + 32% in oak), mid-sized dead wood (+110% in fir, + 94% in oak), large dead wood (+68% in fir, + 99% in oak), standing dead wood (+64% in fir, +82% in oak), ground-lying dead wood (+107% in fir, + 196% in oak), large standing dead wood (+105% in fir, +32% in oak), as well as dead wood diversity (+20% in fir, + 38% in oak). All these effects were significant in fir stands, while only the volume of all dead wood and dead wood diversity increased with dieback in oak stands (Fig. S4.1). The increase in fresh dead wood with dieback level (+69% in fir, +79% in oak) was significant in oak but not in fir forests (Fig. S4.2).

Some individual eco-morphological traits of dead wood displayed significant responses to dieback. Increasing dieback resulted in a significant increase in mean decay stage (ca + 50%) and a decrease in mean position, in both fir and oak forests (Fig. S4.2). In addition, the variance in position and decay stage increased significantly with dieback in both fir and oak forests (Fig. S4.1). The mean and variance of dead wood diameter did not change significantly with increasing dieback in both fir and oak forests (Fig. S4.2).

Table S4.2 – PERMANOVA results (adonis R-function) analysing tree type assemblages (living and dead; top) and TreMs assemblages (bottom) according to forest dieback gradient. Analysis for the whole dataset was constrained by regions and analyses for data subsets (Loire and Pyrenees) were constrained by site.

Context	Df	F.Model	R ²	p.value
Woody elements				
Oak-dominated forests	1	0.6	0.036	0.818 ns
Fir-dominated forests	1	4.4	0.095	0.003 **
Tree-related microhabitats				
Oak-dominated forests	1	1.84	0.103	0.12 ns
Fir-dominated forests	1	4.24	0.092	0.02 *

* = $p < 0.05$; ** = $p < 0.01$

Total γ -diversity (Fig. S4.3) and trait-based gamma diversity (Tab. S4.4) of woody elements were strongly higher in severely declining stands than in healthy and weakly declining ones in fir and oak forests. The contribution of within-site between-plot β_1 diversity to γ -diversity of dead wood types was significantly higher in declining than in healthy stands in fir but not in oak forests (Fig. S4.3). Intra-class between-plot dissimilarity of woody element assemblages was on average significantly higher in the declining stand group compared to healthy stands, in fir forests but not in oak forests (Fig. S4.6). In contrast, intra-class dissimilarity decreased for dead wood only in response to dieback, in fir forests but in oak forests (Fig. S4.7).

Dieback intensity had a significant effect on dead wood assemblage composition in fir forests, but not in oak forests (Tab. S4.2). Several types of dead wood were characteristic of fir stands with medium and high levels of dieback: lying, fir, medium-size, decay class 3 (Tab. S4.3). No dead wood type was significantly characteristic of healthy or slightly declining stands in fir and oak forests, or of severely declining stands in oak forests.

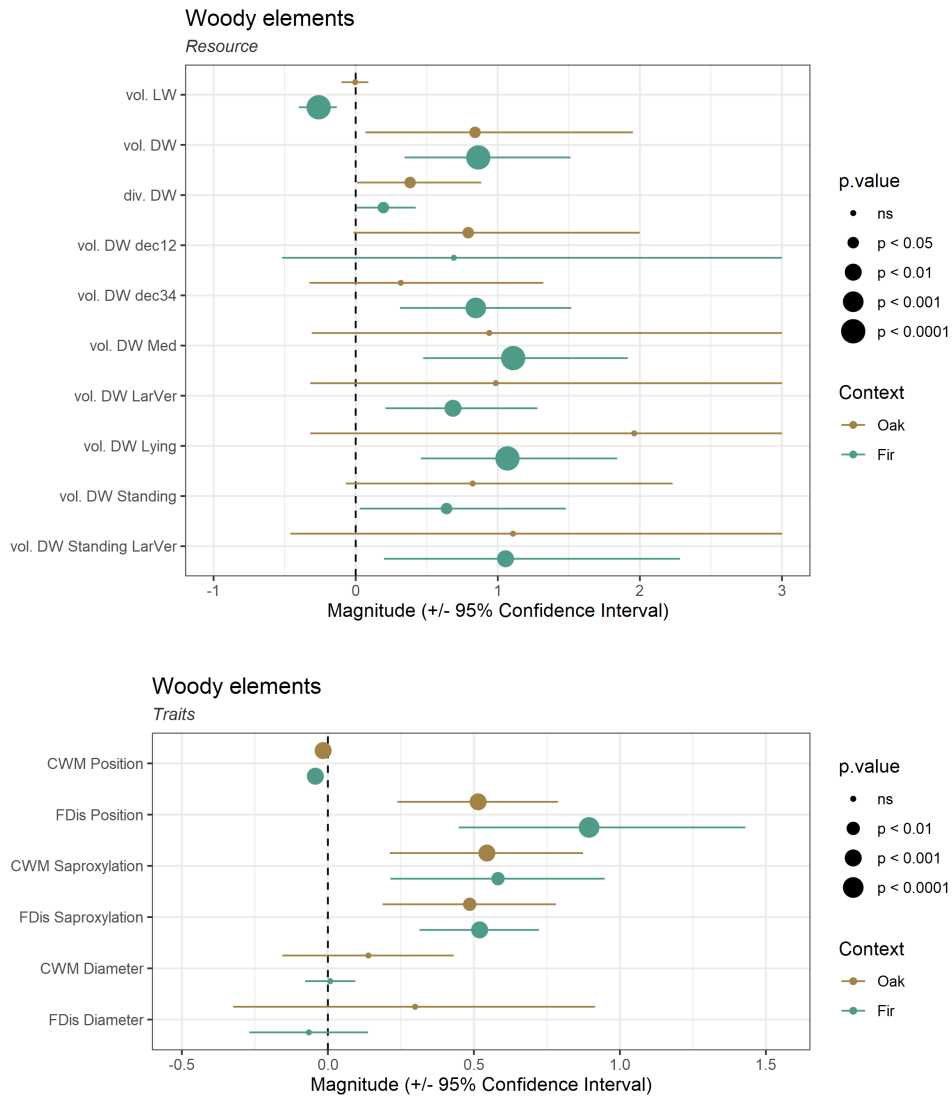


Figure S4.2 – Magnitude from models of the effect of forest dieback level on several variables describing woody biomass resource (top) and traits (bottom). The magnitude is calculated as the increase or decrease in the proportion of woody biomass for a 15% (= SD value) increase in the level of dieback. Point size indicate the model significativities. "LW" = "living wood", "DW" = "dead wood", "vol." = "volume", "dec" = "decay", "Med" = "Mid size dead wood", "LarVer" = "Large and Very large dead wood"; "Position" and "saproxylation" CWM and FDis, as well as functional richness, divergence and evenness include living and dead types of wood while "diameter" CWM and FDis only include dead types of woody biomass.

Table S4.3 – Results from "indicator species" analysis (multipatt R-function) with no restrictions in group combinations. The analysis was only based on dead wood pieces.

Context	Group	Indicator type	A	B	Stat	p.value
Dead wood pieces						
Oak-dominated forests		NA				
Fir-dominated forests	Mid & High	Lying DW, Abies alba, mid-size, decay 3	0.84	0.84	0.842	0.001 ***
Tree-related microhabitats						
Oak-dominated forests	Mid & High	Foliose or fruticose lichens	1	0.55	0.74	0.035 *
Fir-dominated forests	Mid & High	Crack	1	0.24	0.49	0.049 *

"DW" = "dead wood"; * = $p < 0.05$; *** = $p < 0.001$

Table S4.4 – Traits gamma diversity from traits of woody elements (both living and dead materials) and TreMs using kernel gamma R function.

Context	Group	Woody elements	Tree-related microhabitats
Oak-dominated forests	Low	0.008	0.002
	Mid & High	0.039	0.0022
Fir-dominated forests	Low	0.002	0.0034
	Mid & High	0.037	0.0037

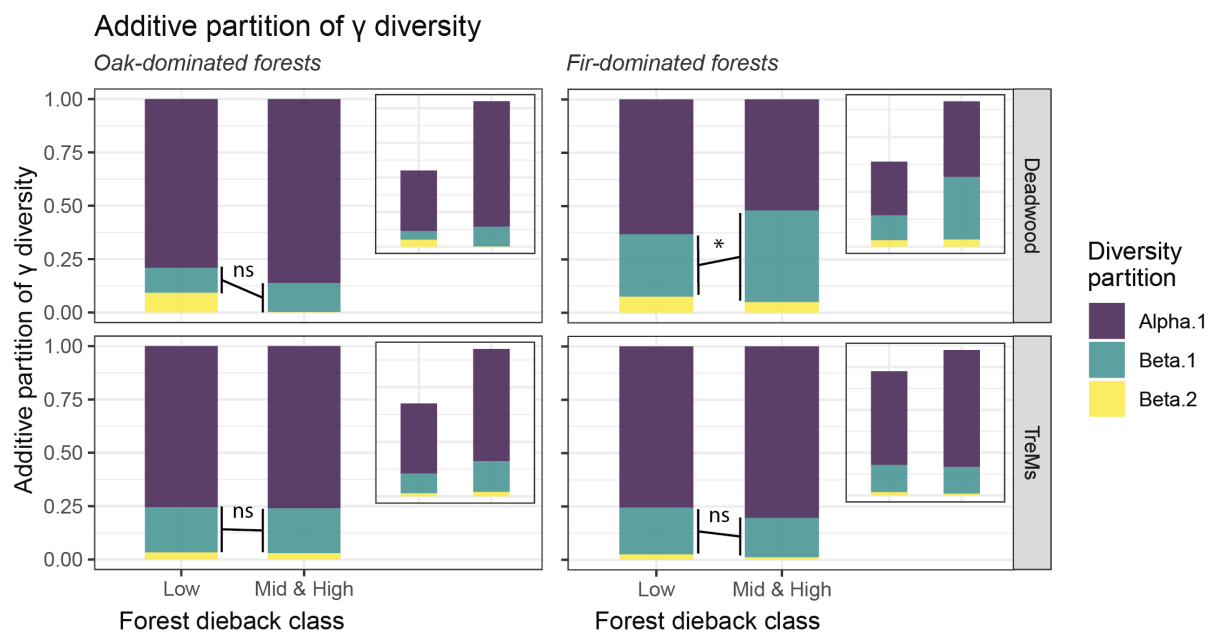


Figure S4.3 – Decomposition of total gamma diversity (of dead wood type and TreMs) using the additive partition R function, into alpha and beta diversity. Beta.1 represent the β -diversity among plots while Beta.2 is the β -diversity among sites (Orléans and Vierzon, Aure and Sault). Tests were done between relative beta diversity among plots (ns = "non-significant difference"; * = "significant difference at 5% α -error rate").

B.3.2 Response of tree-related microhabitats to dieback level

We did not observe significant variations in either local abundance or diversity of TreM-bearing trees with increasing dieback level (Fig. S4.4). The density of trees bearing cavities, epiphytes, burr/canker, exsudates, and crown dead wood was not related to dieback intensity (Fig. S4.4). The density of TreMs

associated to tree bark injuries (i.e. exposed sapwood and heartwood) significantly increased with dieback in fir forests (Fig. S4.4). Likewise, we measured a significant increase in the density of lignicolous fungi (Fig. S4.4), i.e. ephemeral fungi in fir forests (+ 131% for a 15% increase in local dieback level) or perennial fungi in oak forests (+ 105%).

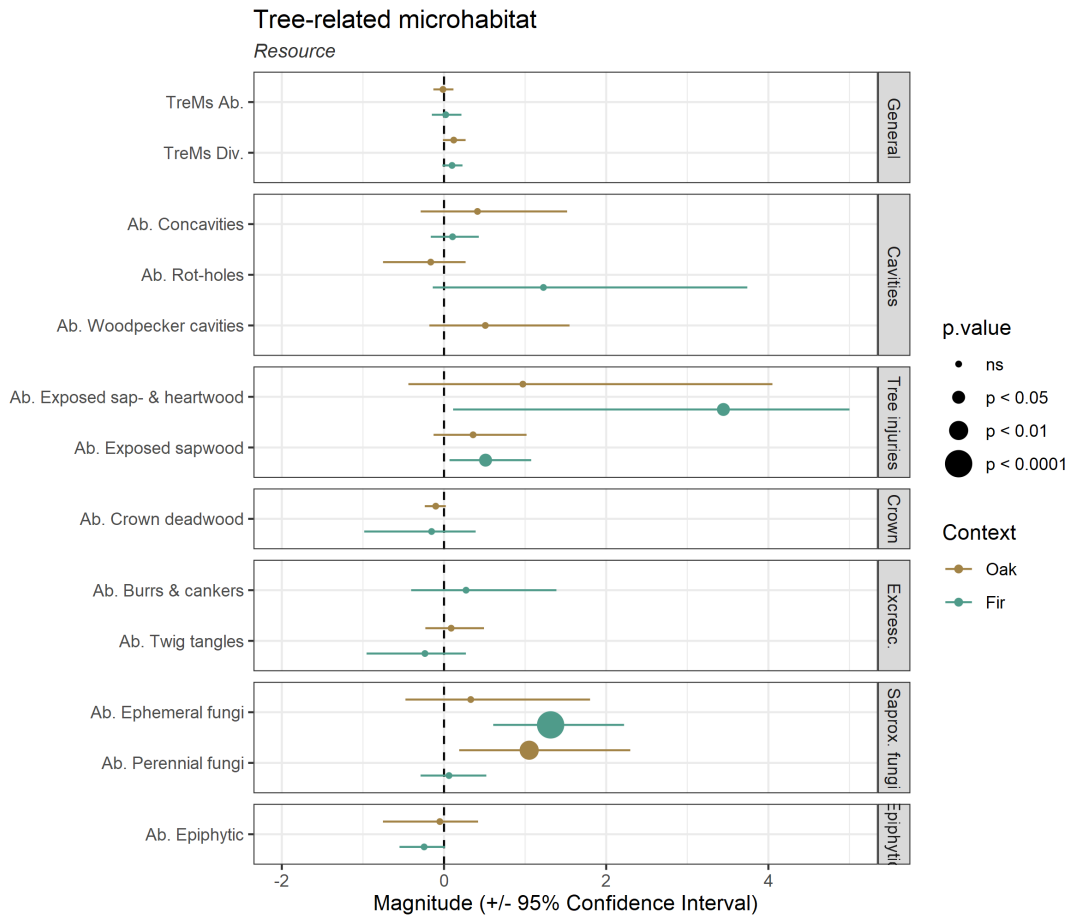


Figure S4.4 – Magnitude from models of the effect of forest dieback level on tree-related microhabitats (TreMs). The magnitude is calculated as the increase or decrease in the proportion of abundance of each TreM for a 15% increase in the level of dieback. Point size indicate the model significativities.

The multi-trait functional dispersion of TreMs did not vary with dieback in oak forests (Fig. S4.5) and increased significantly with dieback in fir forests (+10% ; Fig. S4.8). Only a few effects of dieback on mean trait of TreM assemblages were observed in oak forests (Fig. S4.5), where TreM assemblages were significantly less associated to logs or living trees.

In contrast, several individual eco-morphological traits of TreMs showed significant variations directly in response to increasing dieback in fir forests. Although the decrease in mean of the life span trait was not significant (Fig. S4.8), TreM assemblages were on average more ephemeral (but not significantly) and significantly less perennial in declining stands compared to healthy stands (Fig. S4.5). The mean of ontogenesis trait decreased significantly with increasing dieback (Fig. S4.8); TreM assemblages were on average significantly more rapid-appearing and less slowly-appearing (Fig. S4.5). In line with a significant increase in mean of substrate trait with dieback (Fig. S4.8), we measured that TreM assemblages were significantly less associated to logs and snags (Fig. S4.5). In the absence of a significant increase in mean of the position trait (Fig. S4.8), we did however notice that TreM assemblages were slightly and

significantly more associated with crowns (+8%, Fig. S4.5), and less with lower bole sections (-5%). The epixylic trait of TreM assemblages slightly and significantly decreased in mean in declining stands (-10%), and the increase in the mean saproxylic trait (+21%) of TreM assemblages was slightly significant (Fig. S4.5). The mean and variance of the wetness trait were not influenced by dieback (Fig. 9), and TreMs were not more dry-related or wet-associated on average (Fig. S4.5).

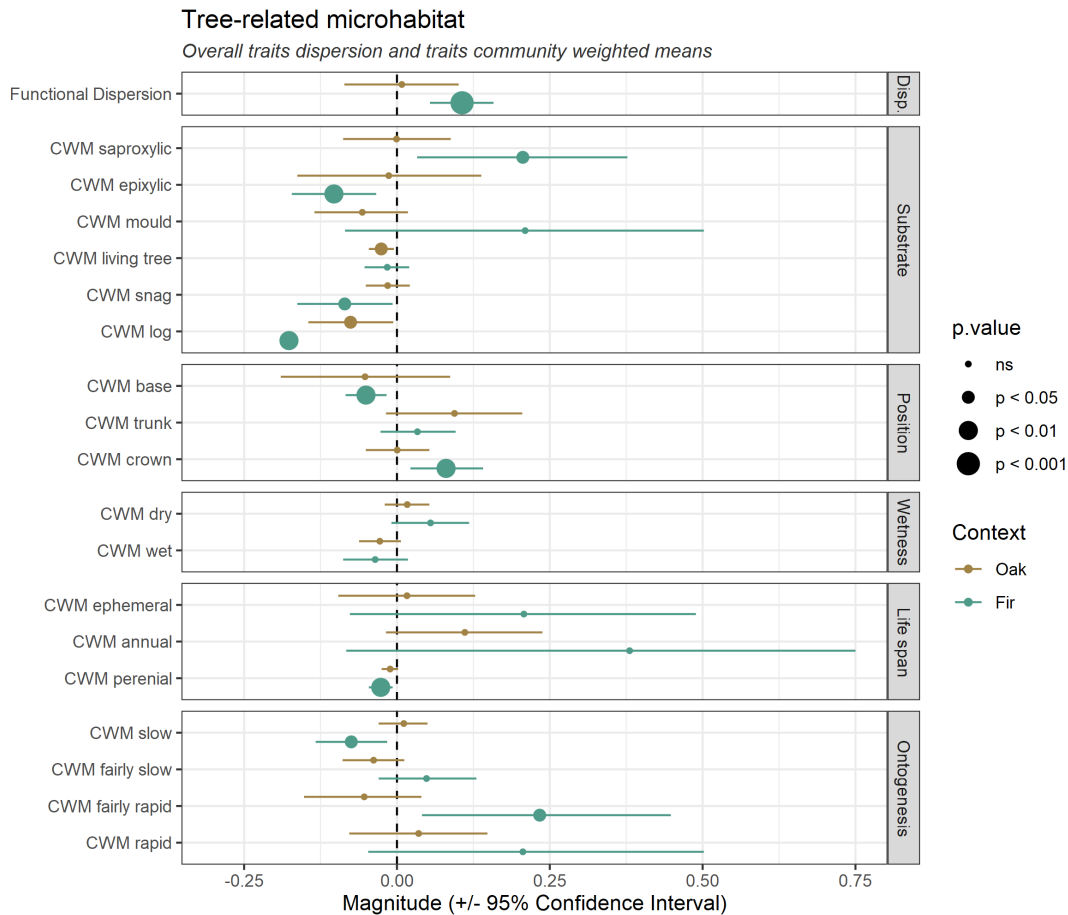


Figure S4.5 – Magnitude from models of the effect of forest dieback level on tree-related microhabitat (TreM) traits. The magnitude is calculated as the increase or decrease in the proportion of abundance of each TreM for a 15% increase in the level of dieback. Point size indicate the model significativities.

Total γ -diversity of TreMs was higher in highly declining vs healthy stands, only slightly in fir forests but largely in oak forests (Fig. S4.3). Functional gamma diversity of TreMs was equal in declining and healthy forests (Fig. S4.5; Tab. S4.4). The contribution of β_1 within-site between-plot diversity to γ -diversity of TreMs was not higher in declining than in healthy stands, neither in silver fir nor in oak forests (Fig. S4.3). Mean between-plot intra-class dissimilarity of TreM assemblages was significantly higher in highly declining than in healthy stands, in both fir and oak forests (Fig. S4.6).

Dieback intensity had a strong and significant effect on Trem assemblage composition in fir forests, but only a slight non-significant effect in oak forests (Tab. S4.2). Only a few TreMs were significantly characteristic of severely declining stands: cracks in fir forests, foliose/fructicose lichens in oak forests (Tab. S4.3). No TreM was characteristic of healthy or weakly-declining stands.

B.3.3 Response of tree-related microhabitats to changes in local dead wood assemblages

The composition of dead wood and TreM assemblages significantly covaried along the stand-level dieback gradient, in fir and in oak forests (Tab. S4.5). Thanks to structural equation modelling, the response of some TreMs was related to dieback-induced changes in dead wood assemblages in fir-dominated forests (Fig. S4.8), as indirect dead wood-mediated effects of dieback. These TreMs were positively associated to dead wood features that were themselves increased by dieback: the multi-trait functional richness of TreM-bearing trees with the volume of mid-sized dead wood, the mean of the ontogenesis trait with the volume of decayed dead wood, the abundance of TreMs, the mean of the life span trait and the variance of the wetness trait with the mean decay stage trait of dead wood (Fig. S4.8).

Table S4.5 – Results from correlation of ordination matrix of woody elements and TreMs (protest R-function).

Context	Correlation in a symmetric Procrustes rotation	Significance
Oak-dominated forests	0.5338	0.02 *
Fir-dominated forests	0.4124	0.001 ***

* = $p < 0.05$; *** = $p < 0.001$

A single TreM feature was positively related to dead wood parameters that decreased with increasing dieback: TreM abundance with the volume of living trees. By contrast, several TreM responses were positively linked with changes in dead wood that were not significantly fostered by the dieback intensity: the diversity of TreMs and the variance of the life span trait with the volume of standing dead wood, the multi-trait functional richness with an increasing mean diameter trait of dead wood, the mean of the saproxylic trait with the diversity of dead wood.

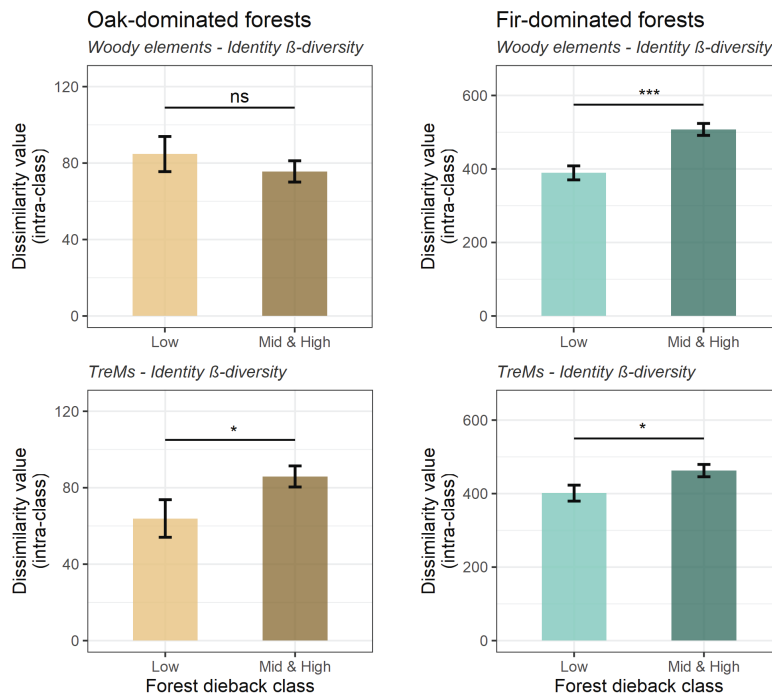


Figure S4.6 – Mean values of intra-class (i.e. forest dieback class) dissimilarity values for assemblages of woody elements (including living trees and dead wood pieces; top) and of tree-related microhabitats (TreMs; bottom) for each study case (oak on the left and Silver fir on the right) using anosim R-function. Error bars indicate standard errors (se). ns = $p > 0.05$, * = $p < 0.05$, *** = $p < 0.001$

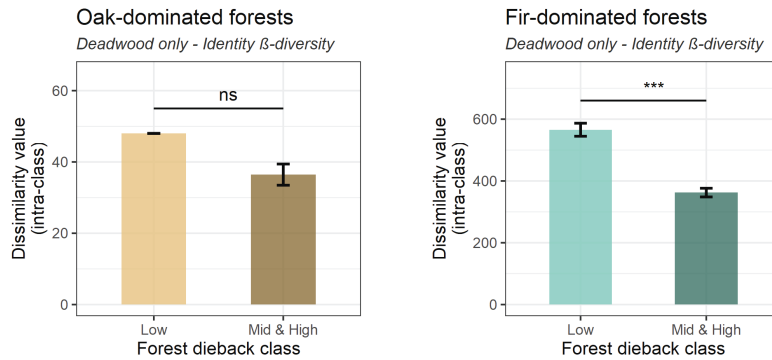


Figure S4.7 – Mean values of intra-class (i.e. forest dieback class) dissimilarity values for assemblages of dead wood only for each study case (oak on the left and Silver fir on the right) using anosim R -function. Error bars indicate standard errors (se). $ns = p > 0.05$, $*** = p < 0.001$

B.4 Discussion

Drought-induced dieback had significant effects on dead wood and tree-related microhabitat assemblages in fir and in oak forests. Dieback effects sound stronger in fir forests than in oak forests, for two kinds of potential reasons related to differences between oak and fir in our study. First, our sampling effort was sharply lower in oak forests, which may lead to non-significant variations despite high magnitude values. Second, due to higher economic stakes and easier access, silviculture in the lowland oak forests is more "dynamic" than in the mountain fir forests and salvage logging is quick and frequent, hiding dieback effects by harvesting disturbance legacies.

B.4.1 Dieback-driven changes in habitat structure

Dead wood

Natural disturbances are known to create biological legacies of various quality. The role of disturbance events on stand structure and composition has already been emphasized (e.g., Nagel et al., 2014). Our results show that drought-induced dieback had similar and strong effects on dead wood stocks in silver fir and oak forests. As expected, droughts promoted the accumulation of dead wood resources, such as fallen branches, standing dead trees and snags, and caused a 80% increase in the volume of all dead wood in declining stands compared to healthy stands.

From Bujoczek and Bujoczek (2022), the extent of damage to living trees by pathological symptoms adversely affecting their health was one of the main significant factors influencing dead wood stocks throughout Polish forests. By killing branches and trees, disturbances allow transient accumulations of dead wood resources (Bouget and Duelli, 2004; Kulakowski et al., 2017; Lindenmayer et al., 2012; Meigs et al., 2017; Schoennagel et al., 2008; Swanson et al., 2011; Thom et al., 2017a; Thorn et al., 2017), already partly discussed in a companion study focusing on silver fir data (Cours et al., 2021). Furthermore, from our ordination results, changes in dead wood type composition were significant in fir but not in oak forests. Overall, all diameter classes significantly increased in declining stands, so that the mean diameter of dead wood assemblages was not affected by dieback.

However, from our results about magnitude values of changes, some dead wood types were more affected by disturbance than others. In oak and fir forests, the strongest changes relate to ground-lying dead wood. In the dead wood profile, the mean dead wood position decreased whereas the mean decay stage increased. In fir forests, mid-sized dead wood and large standing dead wood, rooting from declining

trees, also largely increased in declining stands. Similarly, Spies et al. (1988) already highlighted the importance of large dead wood of variable decay stage as key elements increasing structural complexity in temperate forests after stand-replacing disturbance.

Tree-related microhabitat assemblages

Damage to tree health associated to increased canopy openness may also favour the creation of several tree-related microhabitats (TreMs), such as bark scratches, cracks, broken branches, and cavities in declining trees (Courbaud et al., 2022; Larrieu et al., 2021; Ojeda et al., 2007). Drought can induce progressive tree decline and even tree mortality, under severe water constraints, and thus result in snags accumulating diverse TreMs (Asbeck et al., 2022). Overall, we did not measure a dieback-induced increase in local abundance of TreM-bearing trees. Nonetheless, we observed variations in accumulation of TreM-bearing trees depending on eco-morphological traits. In declining stands compared with healthy forests, TreM assemblages were on average less perennial and more ephemeral, less slowly-appearing and more rapid-appearing, less log and less tree-basis associated and slightly more crown associated.

Contrary to expectations, the mean saproxylic trait of TreM assemblages did not significantly increase with dieback, maybe in line with their slow ontogenesis or with their high susceptibility to management. Likewise, the mean wetness trait of TreM assemblages did not significantly increase in more opened declining stands, which means that despite higher sun exposure, no drying effect occurred. Similarly, the local density of exudate-bearing trees did not vary with dieback. On the one hand, it should be noted that most sap exudates are actually related either to an internal injury or to a problem of excessive internal pressure, unlikely to happen to a dying tree. On the other hand, attacks by certain insect pests may generate sap exudates, but were probably not enough active on study areas. In the same way, the density of trees bearing cavities was not related to dieback intensity. It is nevertheless acknowledged that the degree of crown dieback is a primary variable explaining woodpecker tree selection for cavity excavation (Dudinszky et al., 2021; Ojeda et al., 2007). Regarding such a TreM with slow ontogenesis, time elapsed since major disturbance may be crucial. As a whole, slowly-appearing TreMs, often associated to living trees, were more characteristic of non-declining stands (see above). In contrast, trees bearing lignicolous fungi were significantly more abundant in declining stands in fir and oak forests, since climatic events, which episodically reduce vigour, trigger increased fungal attacks at different tree heights (Ojeda et al., 2007).

Surprisingly the density of trees bearing crown dead wood did not increase with dieback intensity in either fir or oak stands. Yet, within-tree cavitation can generate dry branches, partial branch mortality and can trigger an accumulation of dead wood in the canopy in the short-term. A potential decrease in the volume of living trees (potentially harbouring dead branches) could be invoked in fir forests, since the increase in disturbance intensity decreased the persistence of live fir trees as biological legacies, which dampens the diversity of microhabitats borne by living trees in our sampling design. Our TreM protocol gives an insight onto the ecological roles of remnant live trees, also referred to as survivors (Seidl et al., 2014a). Furthermore, from our protocol, crown dead wood was measured only in living trees, and not on dead trees, recorded as standing dead wood. At last, this TreM is probably measured with a poor accuracy, since the upper part of tree crown is more vulnerable to soil drought (Chakraborty et al., 2017) and potentially bear more dead branches than the lower crown, but is less visible by operators from the ground. It should also be considered that oak forests mainly consist in coppice-with-standards stands in our study areas, which means they include large living healthy standard oak trees with large dead branches.

Furthermore, the increase in exposed sapwood and heartwood with dieback intensity in fir forests may be associated to bark peeling after sunburns and water deficits. Moreover, cracks were characteristic

TreMs of declining fir stands, in line with the increase in the density of snags which frequently harbour this TreM.

Dead wood and tree-related microhabitat

The composition of dead wood and TreM assemblages significantly covaried along the dieback gradient in fir (but not in oak forests), which implies a consistent effect of dieback on dead wood and TreM assemblage composition at stand level.

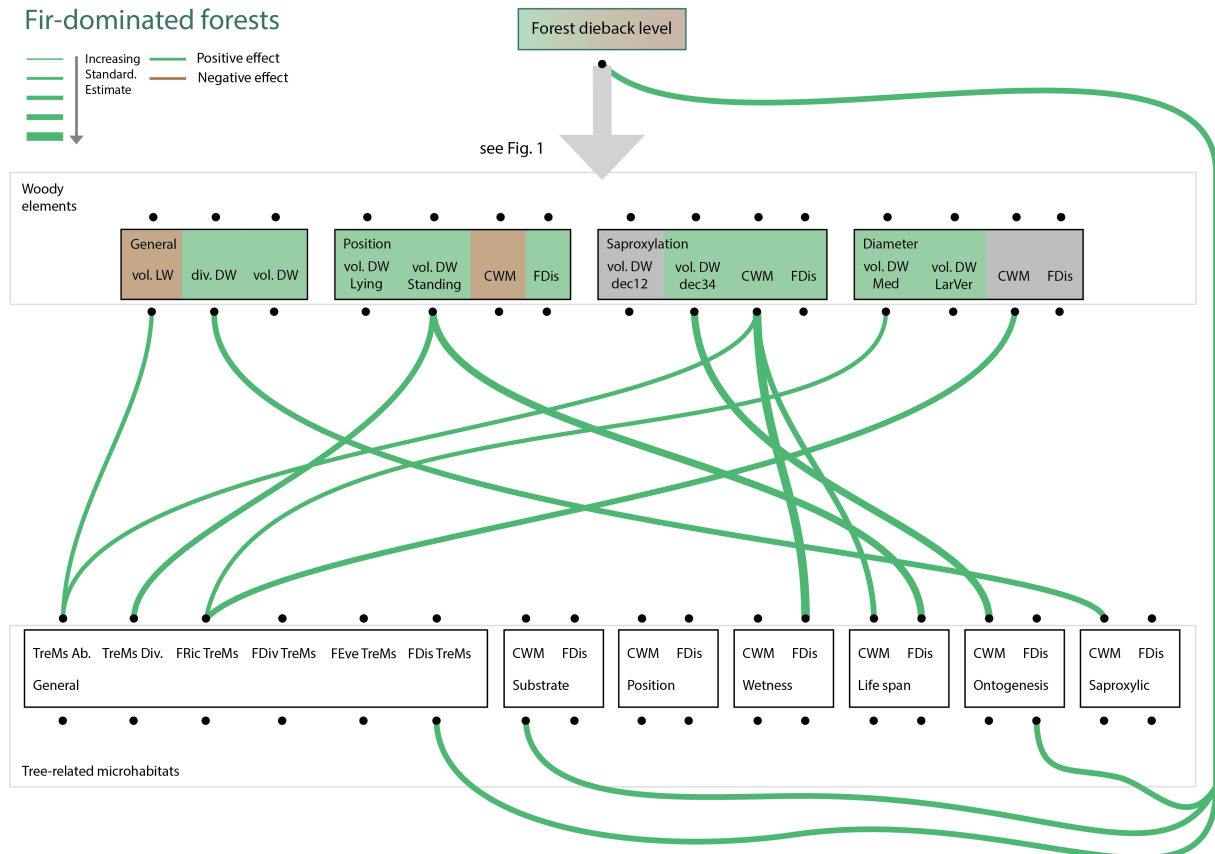


Figure S4.8 – Structural equation modelling (SEM) of forest dieback effects on woody elements and SEM describing the effects of forest dieback and woody elements on tree-related microhabitats. Green = positive effect, brown = negative effect. The thickness of the lines increases with increasing standardized estimates of the SEM. TreM variables being tested for 16 potential effects (effect of forest dieback and woody elements), significant effects are shown at $P \leq 0.003125$. Color boxes for woody elements show the effects of forest dieback in Fig. S4.1: grey = non significant effect, green = significant positive effect, brown = "significant negative effect.

Some of the dieback effects on TreMs were mediated by dead wood features, so that we observed subsequent effects of dieback-induced variations in dead wood elements on TreMs. Logically, TreM diversity increased with the increasing volume of standing dead wood (incl. snags and standing dead trees) and TreM abundance increased with the increase in the mean decay stage trait, maybe in line with more lignicolous fungi on more decayed dead wood pieces.

B.4.2 Diversification of environmental conditions

Several of our results point in the direction of increased local heterogeneity of stand structure by

diversification of dead wood and TreM assemblages in our case studies: (i) dead wood diversity increased with dieback level in fir and in oak forests, (ii) γ -diversity of dead wood types and TreMs were markedly higher in declining than in healthy stands, (iii) variance of dead wood decay stage and dead wood position increased with dieback (in fir and oak forests) for higher heterogeneity in dead wood assemblages, (iv) multi-trait functional dispersion of TreM-bearing trees increased with dieback in fir but not in oak forests. Moreover, other trends related to β -diversity support this heterogenisation effect: (i) the contribution of within-site between-plot diversity to total γ -diversity was significantly higher for dead wood types in declining than in healthy fir stands, (ii) intra-class dissimilarities of woody element assemblages and TreM assemblages were on average significantly higher in the group of declining fir stands compared with healthy stands, (iii) intra-class dissimilarity of TreM assemblages was significantly higher in highly declining than in healthy oak stands.

Natural disturbances have already been demonstrated to generate structural diversity (Turner, 2010), spatial heterogeneity over several embedded scales from trees to landscapes (Seidl et al., 2014a), forest canopy structural complexity (Gough et al., 2022), structural complexity in homogenized landscapes (Kulakowski et al., 2017). From Meigs et al. (2017), complex forest structure – including features nominally associated with old-growth forests – can be associated with disturbance severity. Disturbance legacies, such as standing dead trees, snags, microhabitat-bearing trees and forest-floor dead wood, are key elements of forest structural complexity. Natural disturbances increase the variability of dead wood (Aakala, 2010). Droughts and windstorms promote the diversification of dead wood resources (Swanson et al., 2011; Thorn et al., 2017).

B.5 Conclusion

Accumulation of disturbance legacies and enhanced structural habitat heterogeneity generally benefit forest biodiversity. Disturbances allow transient accumulations of microhabitats and resources, which may be scarce in managed forest ecosystems, and which improve habitat conditions for rare and common species during post-disturbance recovery. Following disturbances, fallen and weakened trees constitute a major pulse of suitable breeding substrates for opportunistic wood-dwelling organisms. Consequently, restoration activities to (re)create old-growth conditions and dead wood enrichment strategies may take advantage of the multiple ecological benefits of disturbances by suggesting the retention of patches of declining and dead trees. Selective post-disturbance logging can maintain some ecologically important structural characteristics. Post-disturbance management should weigh the economic benefits of timber production versus the ecological benefits of disturbance-created complexity. To spare the benefits of disturbances on beneficials, regeneration and biodiversity, and while respecting economic and phytosanitary balances, a retention silviculture could be thought to take advantage of the crisis, aiming at selective salvage logging and preserving a proportion of the biological disturbance legacies. Thorn et al. (2020) provided benchmarks for retention targets, i.e., the proportion of naturally disturbed forest area that should be excluded from salvage logging to maintain biodiversity.

B.6 Acknowledgments

The authors would like to thank C. Moliard and B. Nusillard for their help in data collection, Carlos Lopez-Vaamonde, Lucas Sire and Simon Thorn for fruitful interactions within the Climtree project.

Appendix for "Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests"

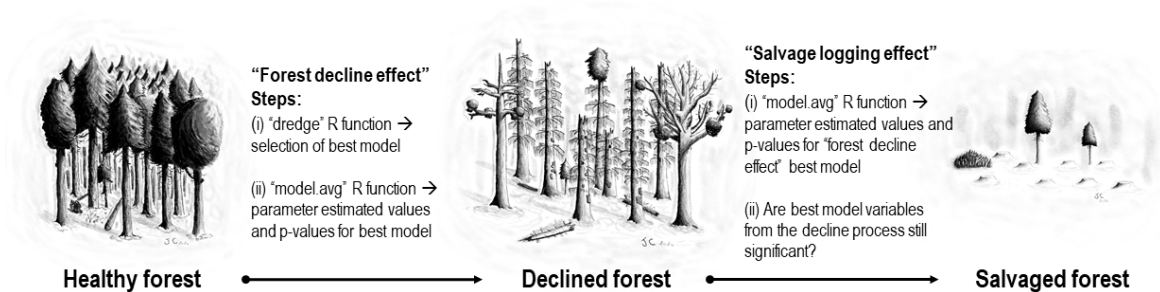


Figure S5.1 – "Process logic" of our data analysis. First: the natural forest dieback process – we assessed the best model (with the dredge function from the MuMin R package) to obtain beta estimates and p-values by "model averaging" with the MuMin R package. Second: the anthropogenic effect (salvage logging) – we carried out "model averaging" on the salvage logging dataset and then checked to see if the variables from the dieback-effect best models were still significant. The objective was to assess how salvage logging changed the ecological relationships between stand features and saproxylic beetle communities.

APPENDIX C. APPENDIX FOR "CONTRASTING RESPONSES OF HABITAT CONDITIONS AND INSECT BIODIVERSITY TO PEST- OR CLIMATE-INDUCED DIEBACK IN CONIFEROUS MOUNTAIN FORESTS"

Table S5.1 – *Table of stand feature effects (deadwood, stand structure and tree-related microhabitats) associated to dieback or salvage logging effects in Pyrenean silver fir forests on saproxylic beetle niche traits (CWM = "community weighted mean"; FD = "functional diversity"). Effects were tested through generalized linear mixed models (with "site" as a random variable). The variables involved in the best model for dieback effects (left panel) were assessed (direction and significance) in the models of salvage logging effects (right panel). "Linear" is a Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy		Disturbed Salvaged +
		Best model	Estimate (β) \pm se	
<i>Niche traits</i>				
CWM wood diameter	Linear	Lying DW diversity 0.3ha	-0.06* \pm 0.03	0.004 ^{ns} \pm 0.02
FD wood diameter	Linear	Lying DW diversity 0.3ha	0.06 ^{ns} \pm 0.04	-0.006 ^{ns} \pm 0.04
CWM wood decay	Linear	Living trees BA 0.3ha	-0.11* \pm 0.05	-0.08 ^{ns} \pm 0.05
FD wood decay	Linear	Large log density 1ha	0.11 \pm 0.04	0.08 ^{ns} \pm 0.05
CWM canopy	Linear	Null model	-0.06* \pm 0.03	-0.04 ^{ns} \pm 0.03
CWM wood decay	Linear	Canopy openness 1ha	-0.09* \pm 0.04	-0.04 ^{ns} \pm 0.04
CWM wood decay	Linear	Living trees BA 0.3ha	0.08* \pm 0.04	0.02 ^{ns} \pm 0.04

Table S5.2 – *Table of stand-feature effects (deadwood, stand structure and tree-related microhabitats) associated to dieback or salvage logging effects in Bavarian spruce forests on saproxylic beetle niche traits (CWM = "community weighted mean"; FD = "functional diversity"). Effects were tested with generalized and general linear models. The variables involved in the best model for dieback effects (left panel) were assessed (direction and significance) in the models of salvage logging effects (right panel). "Linear" is a Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy		Disturbed Salvaged +
		Best model	Estimate (β) \pm se	
<i>Niche traits</i>				
CWM wood diameter	Linear	Large log density 1ha	0.12 ^{ns} \pm 0.07	0.05 ^{ns} \pm 0.04
FD wood diameter	Linear	Log standing DW vol. 0.3ha	0.09* \pm 0.04	-0.002 ^{ns} \pm 0.05
CWM wood decay	Linear	Log DW vol. 0.3ha	0.24** \pm 0.08	0.08 ^{ns} \pm 0.07
FD wood decay	Linear	Living trees BA 0.3ha	0.14** \pm 0.05	0.08 ^{ns} \pm 0.05
CWM canopy	Linear	Lying DW diversity 0.3ha	0.08* \pm 0.04	0.03 ^{ns} \pm 0.04
FD canopy	Linear	Canopy openness 1ha	0.12 ^{ns} \pm 0.06	0.11 ^{ns} \pm 0.06
FD canopy	Linear	Large log density 1ha	0.12* \pm 0.04	-0.03 ^{ns} \pm 0.06

Table S5.3 – *Analysis of between-class dissimilarity of saproxylic beetle assemblages based on Bray-Curtis distance matrices ("adonis" function from the vegan package, Oksanen et al., 2022). Comparison of species assemblage composition between healthy and unharvested disturbed stands (middle column) and between unharvested disturbed and salvaged stands (right column).*

Context	Healthy vs. Disturbed	Disturbed vs. Salvaged
Pyrenees	p = 0.25 ^{ns}	p = 0.12 ^{ns}
Bavaria	p < 0.001***	p = 0.029*

P-values after a 999-run permutation test: *** P < 0.001; * 0.05 > P > 0.01

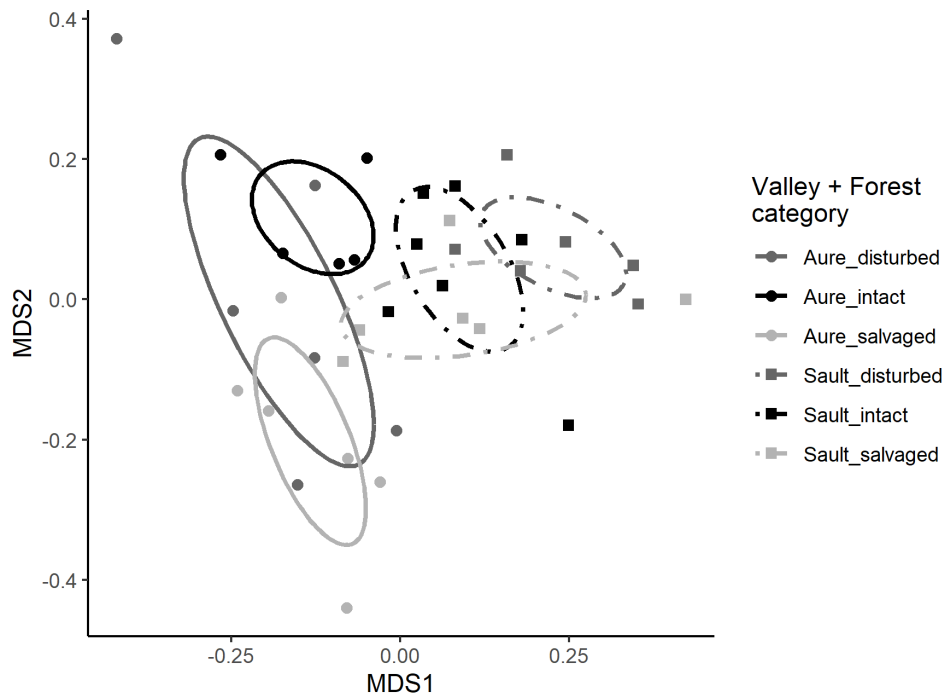


Figure S5.2 – Results of the non-metric dimensional scaling (NMDS) analysis of communities in the Pyrenean *Abies alba* forests.

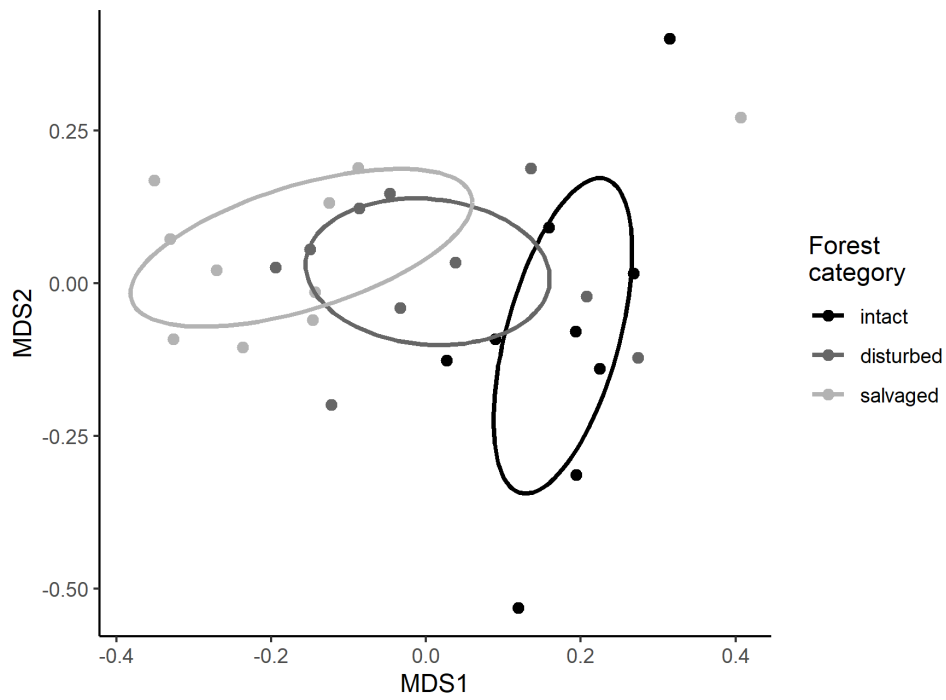


Figure S5.3 – Results of the non-metric dimensional scaling (NMDS) analysis of communities in the Bavarian *Picea abies* forests.

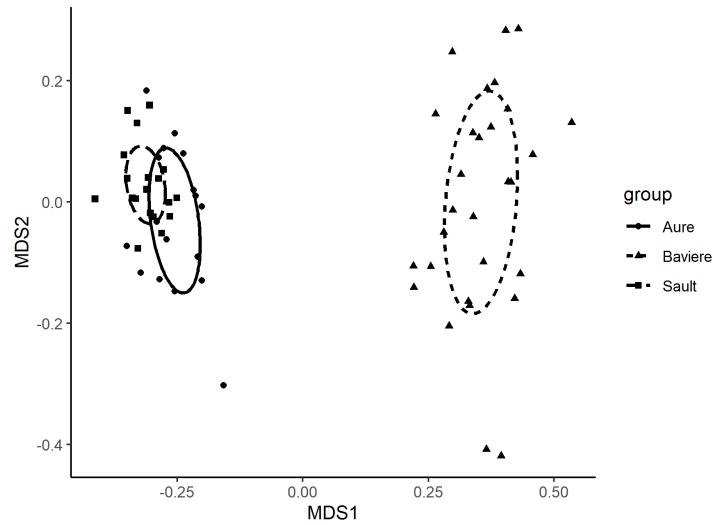


Figure S5.4 – Results of the non-metric dimensional scaling (NMDS) analysis of communities at all study sites.

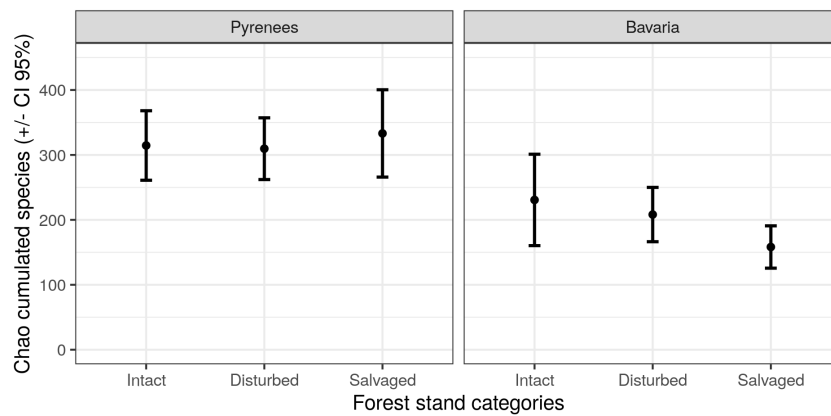


Figure S5.5 – Extrapolated species richness using the Chao method for each country and each forest category. Points represent means and error bars the 95% confidence interval. "Intact" = "healthy"

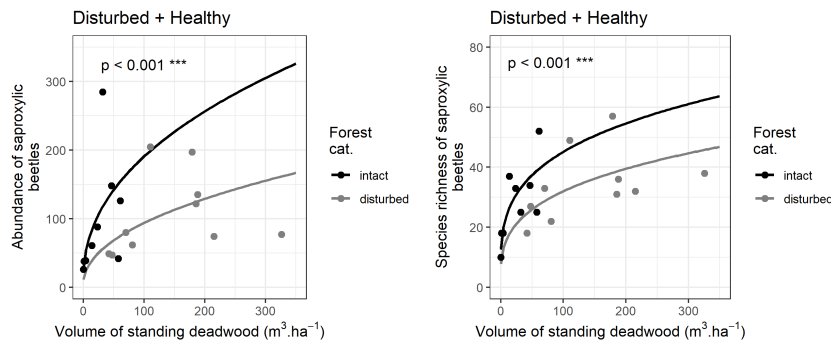


Figure S5.6 – Relationship between volume of standing deadwood in Bavarian spruce forests and abundance of saproxylic beetles as a whole (left); and species richness of saproxylic beetles as a whole (right). Lines are the regression curves from a negative binomial model (with log-transformation of x on the right). "intact" = "healthy"

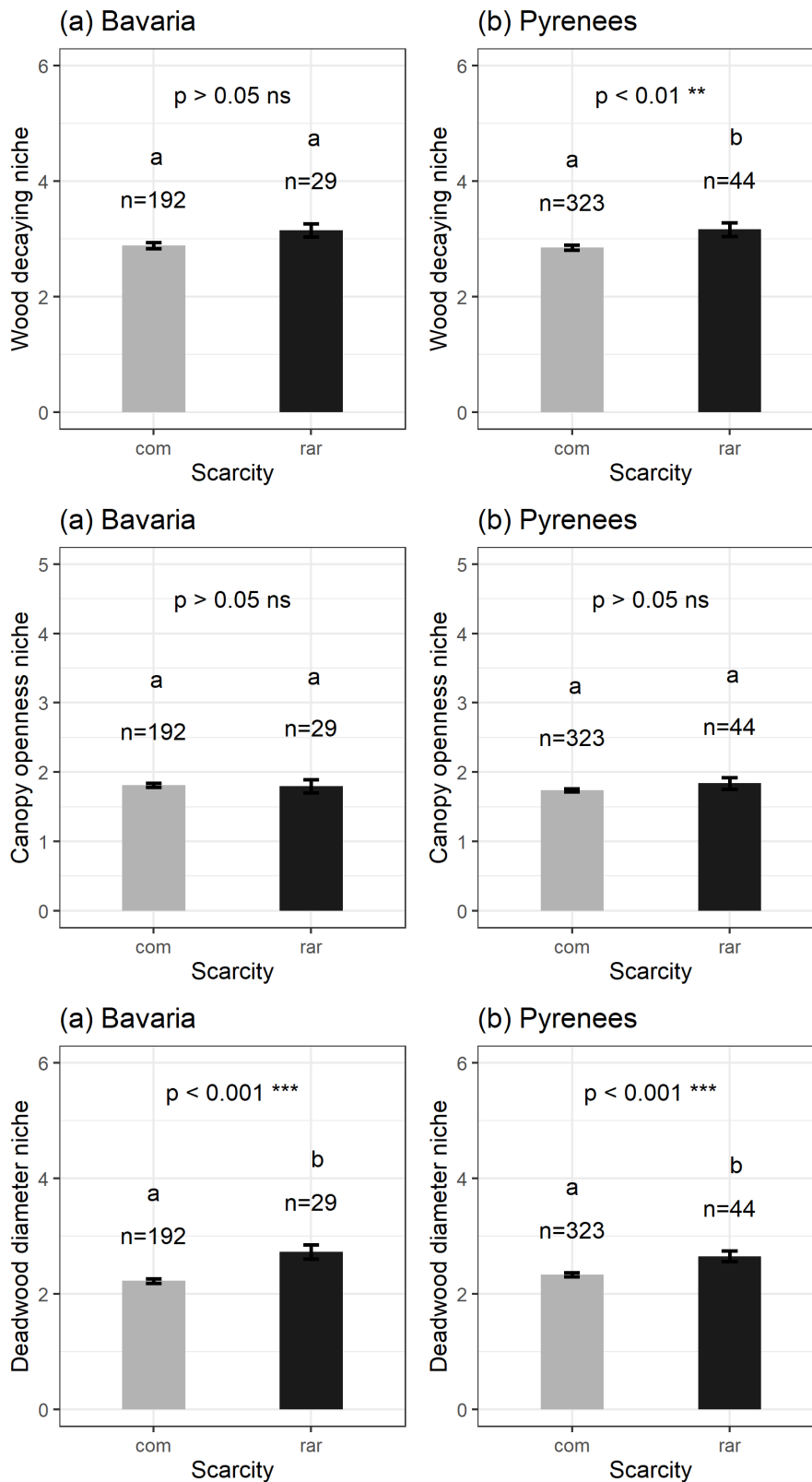


Figure S5.7 – Mean niche occupied by common ("com") and rare ("rar") (red-listed in Bavaria) species captured in Bavaria (a) and the Pyrenees (b). Letters were assigned after a Student's test.

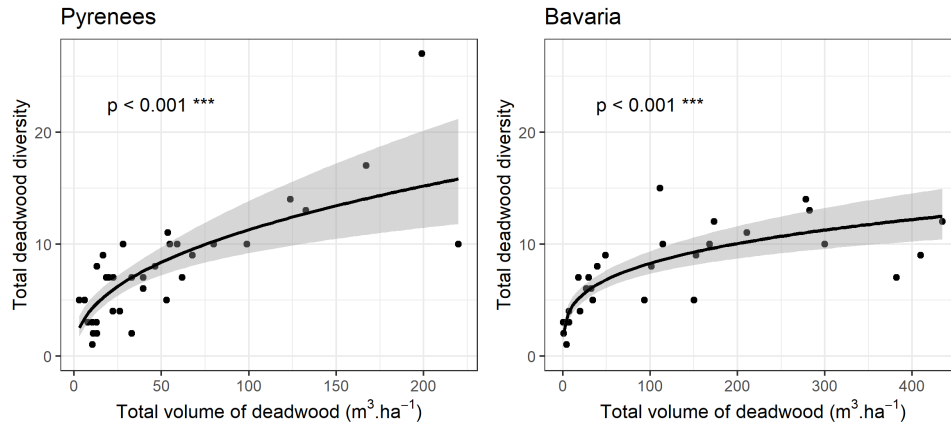


Figure S5.8 – Relationship between deadwood volume and deadwood diversity in the Pyrenean silver fir forest (left) and the Bavarian spruce forest (right). The black line is the regression curve from a negative binomial model and the grey area indicates the 95% confident interval.

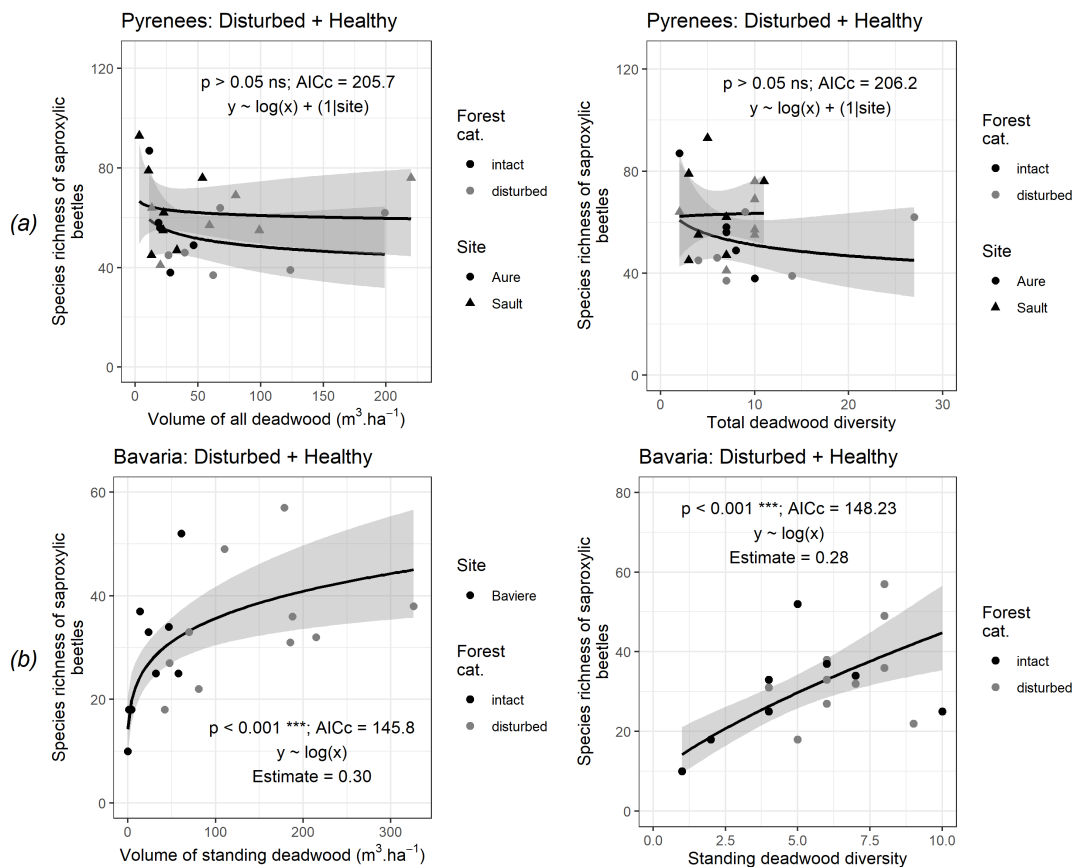


Figure S5.9 – Model comparisons between total saproxylic beetle species richness in each region (Pyrenees = a; Bavaria = b) and (left panels) deadwood volume (reflecting resource quantity) and (right panels) deadwood diversity (reflecting resource diversity). We selected the variable associated with the lowest AICc for each resource quantity variable (all, standing and lying deadwood volume) and for each resource diversity variable (all, standing and lying deadwood diversity). The black line is the regression curve from the negative binomial model and the grey area indicates the 95% confident interval.

(a) Bavaria spruce forest



(b) Pyrenean fir forest



Figure S5.10 – *Pictures of insect-induced forest dieback in Bavaria (left) and climate-induced forest dieback in the Pyrenees (right). The severity of the phenomenon is very different for each of the two cases: very severe in Bavaria, moderately severe in the Pyrenees.*

Appendix D

Appendix for "The living from the dead: changes in taxonomical and functional composition of saproxylic beetles following forest dieback events"

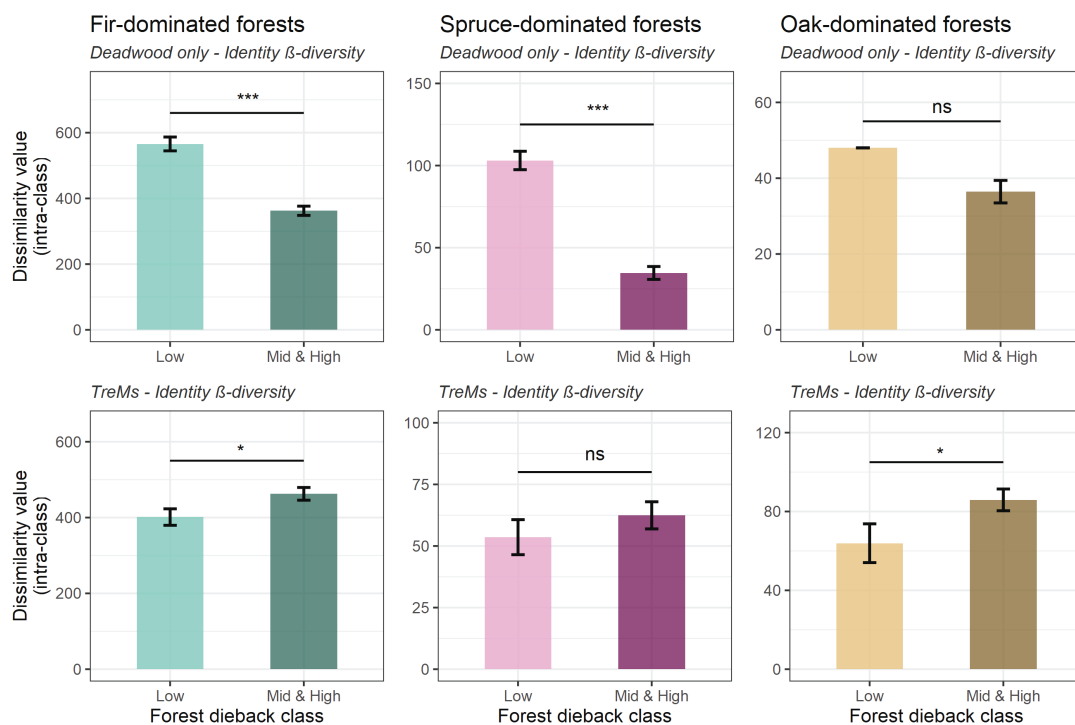


Figure S6.1 – Mean values of intra-class (i.e. forest dieback class) dissimilarity values for assemblages of dead wood only and tree-related microhabitats for each study case using anosim R-function. Error bars indicate standard errors (se). ns = $p > 0.05$, * = $p < 0.05$, *** = $p < 0.001$

APPENDIX D. APPENDIX FOR "THE LIVING FROM THE DEAD: CHANGES IN TAXONOMICAL AND FUNCTIONAL COMPOSITION OF SAPROXYLIC BEETLES FOLLOWING FOREST DIEBACK EVENTS"

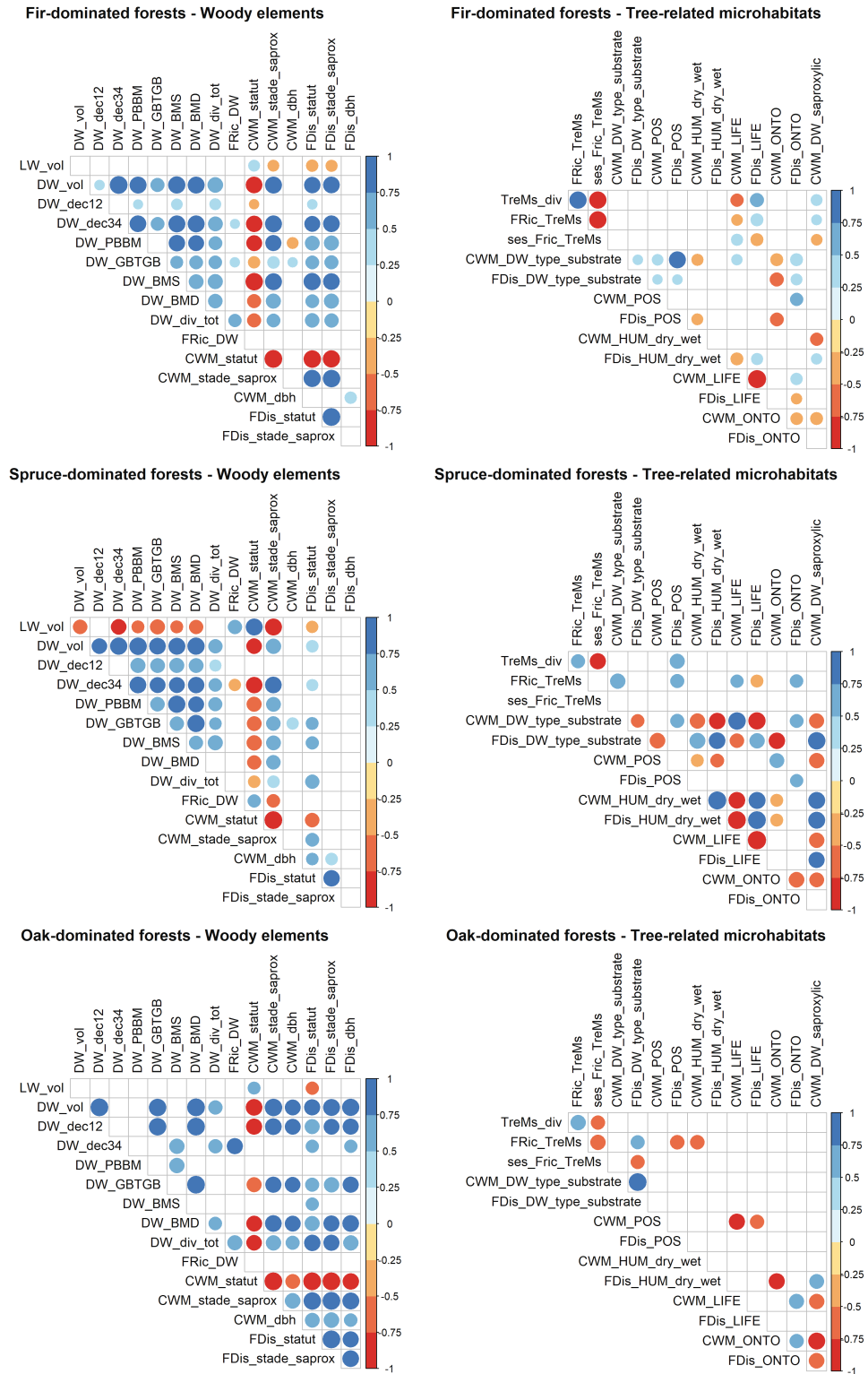


Figure S6.2 – Correlation plots between environmental variables in each context. The correlations showed were selected at $p < 0.05$.

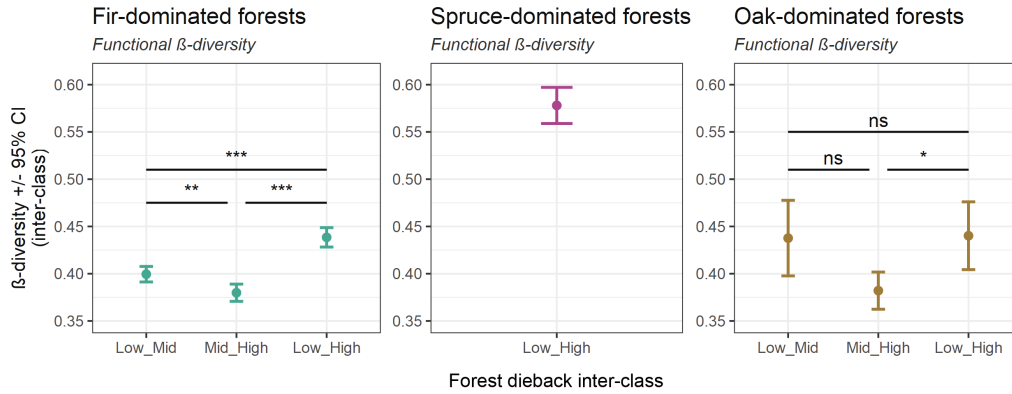


Figure S6.3 – Differences in functional composition between forest dieback classes (inter-class β -diversity) in each study case (left: Pyrenees, middle: Bavaria, right: Loire). For instance, in fir-dominated forests, there are significantly more differences in functional composition between low and high dieback plots, than between low and mid. Mean comparisons of were done using post-hoc Tukey tests. * = $p \neq 0.05$, ** = $p \neq 0.01$, *** = $p \neq 0.001$

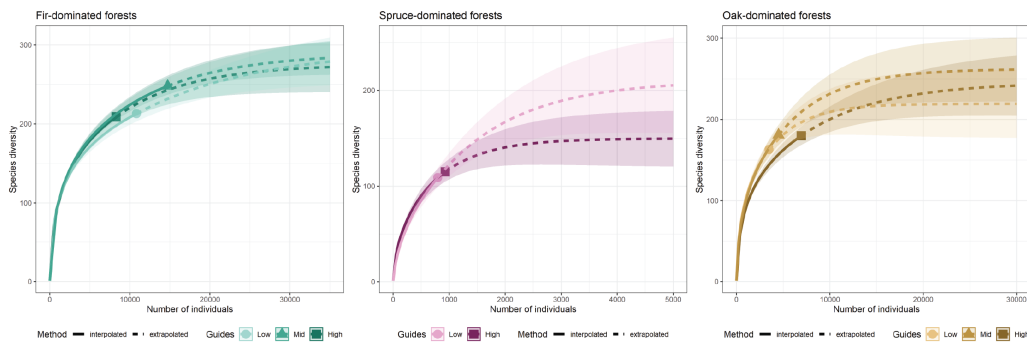


Figure S6.4 – Rarefaction/extrapolation curves of species richness along the gradient of forest dieback intensity and in each study context, with 95% confidence intervals (shading). The resulting estimate of γ -diversity in each dieback class is never different from one class to another.

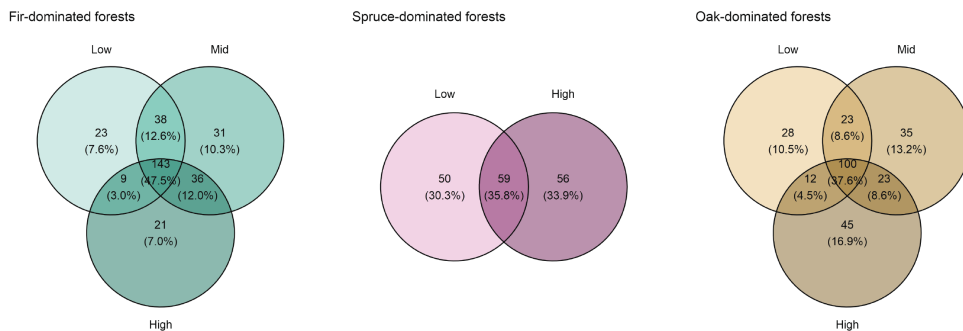


Figure S6.5 – Venn diagram showing the shared sum of saproxylic beetle species between forest dieback classes and the sum of species associated with a single class.

Appendix E

Appendix for "Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales"

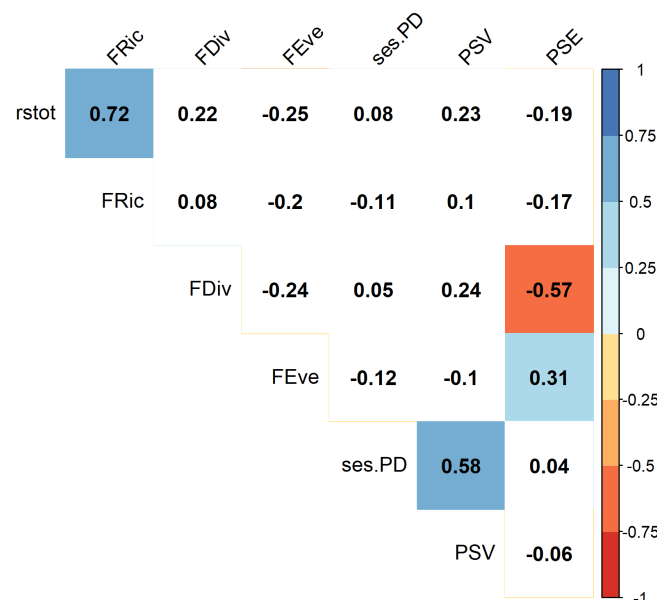


Figure S7.1 – Correlation table for the diversity indices. Coloured relationships are statistically significant at an α -level of 0.05. Blue represents positive correlations while red represents negative correlations. Numbers are the Pearson's r values. See Sect. 7.3.

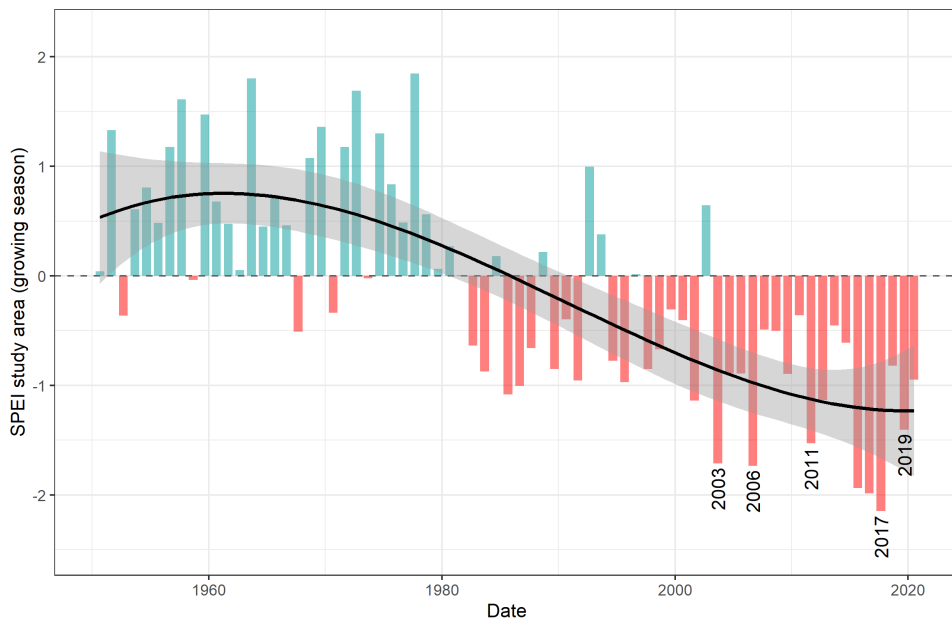


Figure S7.2 – Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) from 1950 to 2020 for the whole study area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

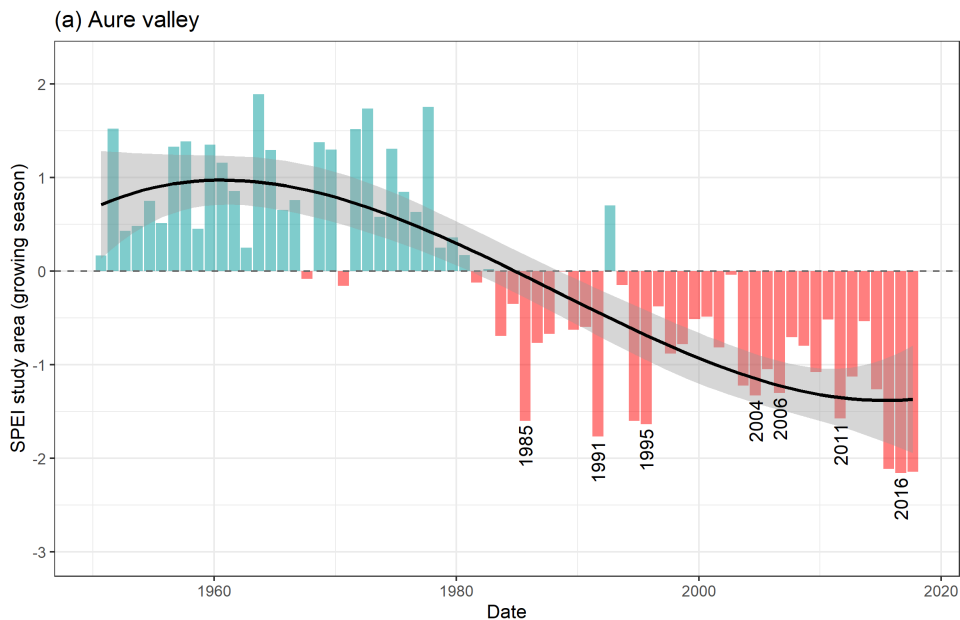


Figure S7.3 – Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) from 1950 to 2020 in Aure Valley area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

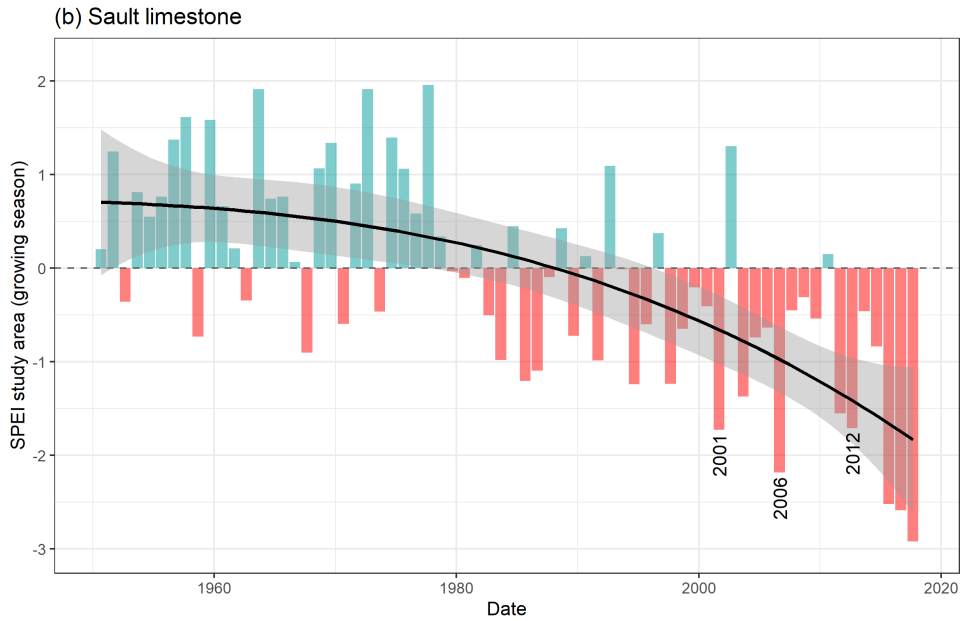


Figure S7.4 – Changes in the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) from 1950 to 2020 in the Sault plateau area. Years marked by severe droughts are given under the corresponding bar; red: negative annual water balance (drought); blue: positive annual water balance (water surplus).

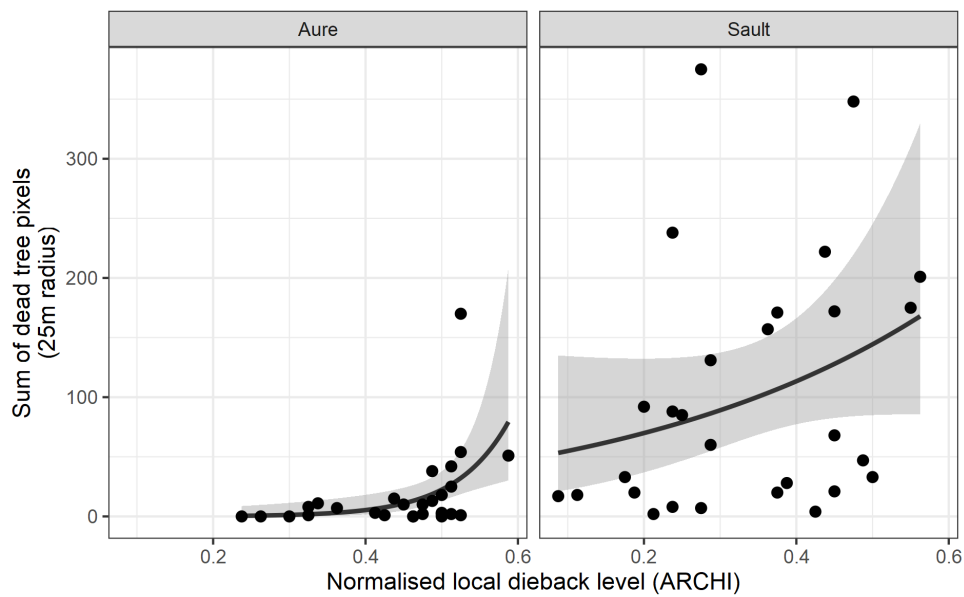


Figure S7.5 – Relationship between the sum of dead crown pixels in a 25m radius around study plot centres (from machine learning) and the actual forest dieback level quantified in the study plots with the ARCHI method.

APPENDIX E. APPENDIX FOR "DROUGHT-INDUCED FOREST DIEBACK INCREASES TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY OF SAPROXYLIC BEETLES AT BOTH LOCAL AND LANDSCAPE SCALES"

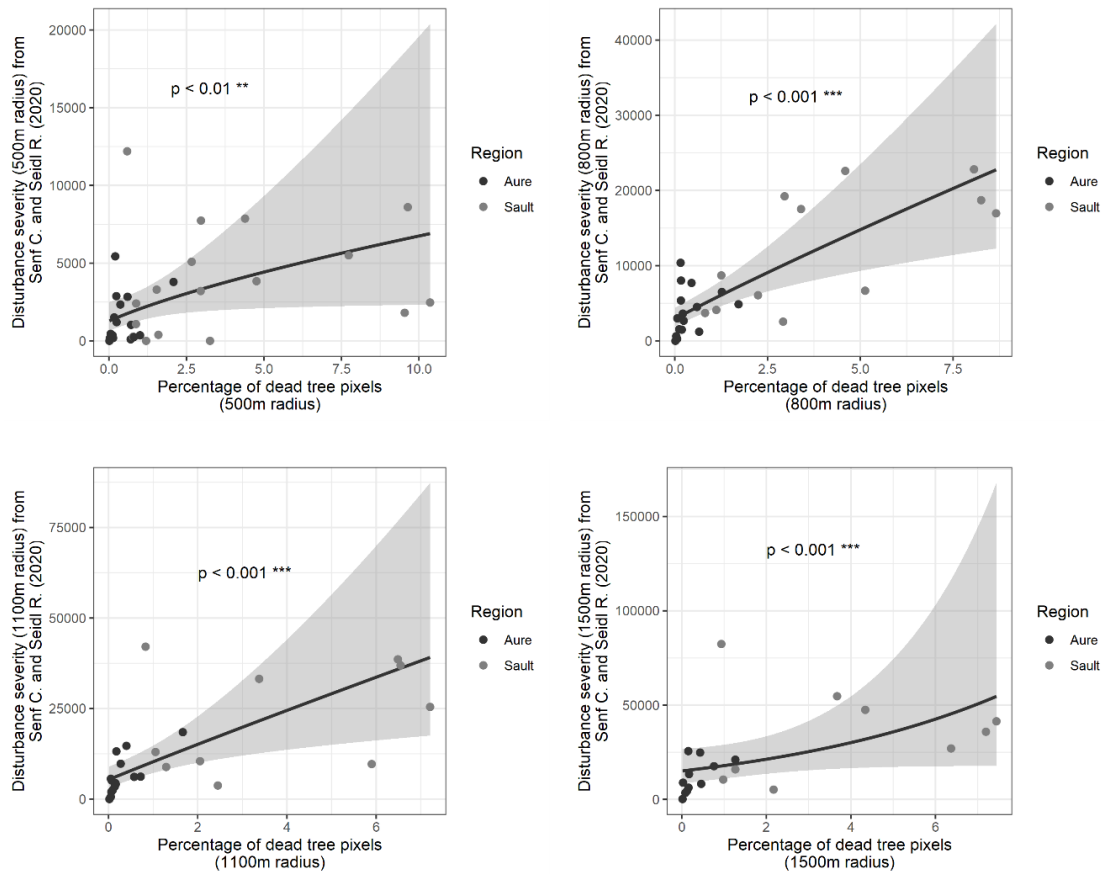


Figure S7.6 – Relationships between the sum of dead crown pixels at different landscape scales around the study plot centres (from machine learning) and the actual forest dieback level quantified in Senf and Seidl (2021a).

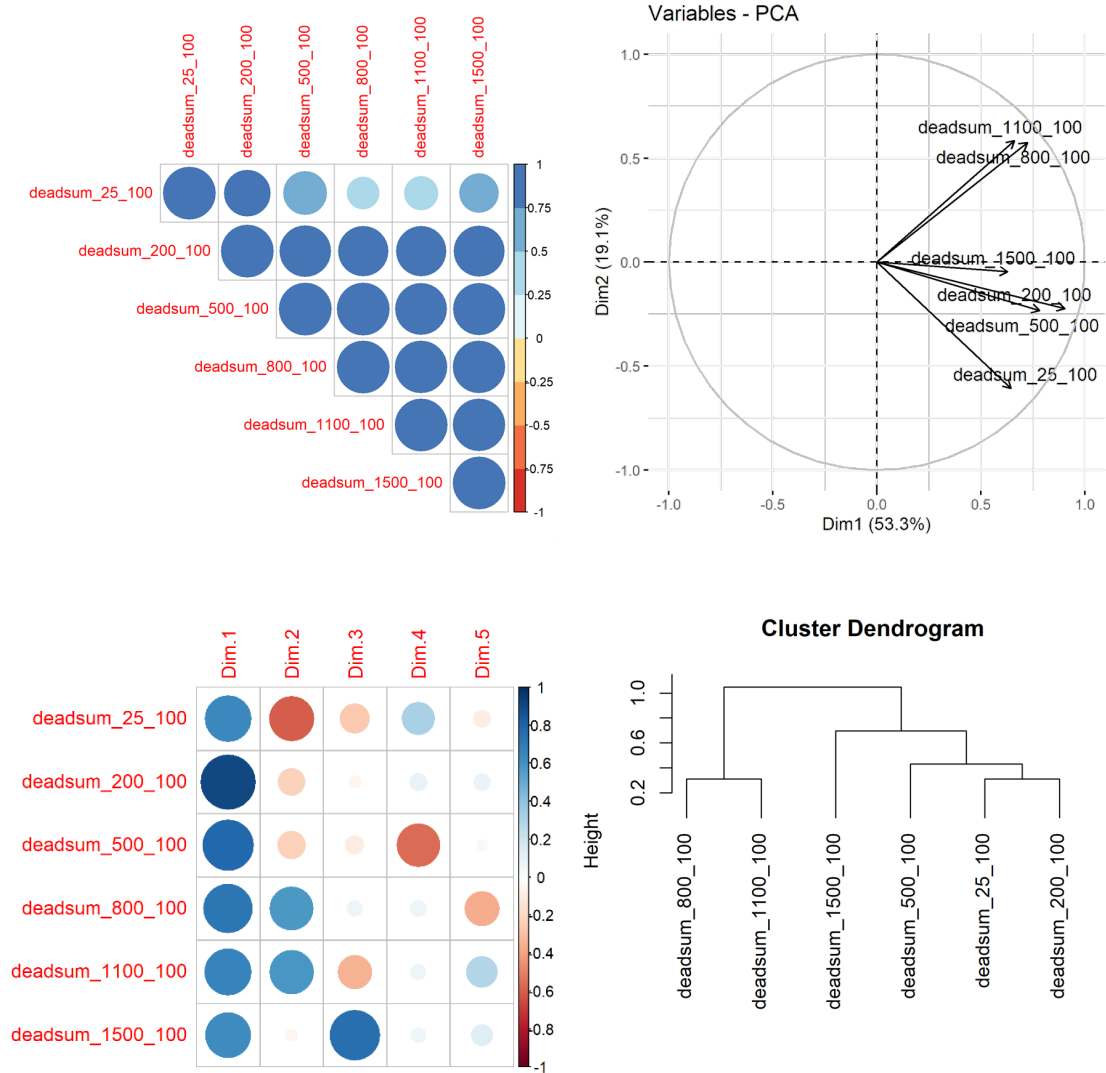


Figure S7.7 – **Above-left:** correlation table with dead crown sums according to different spatial scales. **Above-right:** results from the Principal component analysis (PCA) of all the spatial scales for forest dieback. **Bottom-left:** correlation between the dead crown sums and PCA dimensions at different spatial scales. **Bottom-right:** cluster dendrogram of the dead crown sums at different spatial scales.

*APPENDIX E. APPENDIX FOR "DROUGHT-INDUCED FOREST DIEBACK INCREASES
TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY OF SAPROXYLIC BEETLES AT
BOTH LOCAL AND LANDSCAPE SCALES"*

Table S7.1 – *Pearson’s r correlation coefficients between scales of forest dieback in non-overlapping buffers.*

Scales	25m	200m	500m	800m	1,100m	1,500m
25 m	1	0.78	0.68	0.38	0.41	0.55
200 m		1	0.95	0.91	0.91	0.93
500 m			1	0.99	0.97	0.97
800 m				1	0.98	0.99
1100 m					1	0.99
1500 m						1

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Consequences of dieback in temperate forests on habitat structure and biodiversity

Abstract:

Natural disturbances are an integral part of forest ecosystems. They ensure the creation of new habitats, maintain high spatial heterogeneity and disrupt the ecological succession processes. Forest ecosystems in a particular region are historically adapted to the disturbance complexes affecting that region (i.e. the disturbance regime). They are also largely affected by so-called anthropogenic disturbances (e.g. logging). The process of progressive tree death due to these different disturbances is called "forest dieback". Generally, these diebacks are followed by salvage or sanitation logging to harvest the commercial value of the trees before they deteriorate or to contain future pest outbreaks. This logging is considered to be additional disturbance. However, ongoing changes in climate and land use are leading to changes in the regime of these disturbances. In the extreme, if the change in these regimes is too great, it can lead to a shift towards a non-forest ecosystem. These regime shifts could then result in regional extinctions of forest species and alter the ecosystem services provided by forests to human societies. The study of these forest diebacks is therefore of central importance. In this thesis, we focus on the response of saproxylic beetles (i.e. beetles linked for part or all of their life cycle to dead wood), an ecological group threatened in temperate managed forests due to the scarcity of the dead wood resource. We also analyse habitat changes caused by these diebacks (i.e. disturbance legacies). For this purpose, we study three case studies of European dieback: (i) Pyrenean fir (*Abies alba*) and (ii) Loire Valley oak (*Quercus* spp.) caused by droughts, and (iii) Bavarian spruce (*Picea abies*) caused by storms and *Ips typographus* outbreaks. On each of these sites, we inventoried the dead wood and tree-related microhabitats present on the plots as well as saproxylic beetles. These surveys revealed significant changes in habitats, resulting in increases in dead wood and changes in tree-related microhabitat composition. These changes appeared to be modulated by the severity of dieback. In cascade, these habitat changes induced modifications in the local composition of saproxylic beetles. For both coniferous forests, habitat changes induced positive effects of dieback on local beetle diversity, both taxonomic and functional. Furthermore, we observed generalisation of saproxylic beetle communities in the landscape due to dieback. Furthermore, we highlighted the importance of dieback at the landscape scale on local taxonomic, functional and phylogenetic assemblages of saproxylic beetles. We also show that functional and phylogenetic diversity were mostly driven by landscape processes. Finally, we note that sanitary and salvage logging did not affect local beetle diversity but strongly altered their ecological relationships. Our results highlight the value that can be gained from declining areas for the conservation of otherwise threatened species groups in managed forest areas, by maintaining the habitats created (i.e. dead wood and tree-related microhabitats). Finally, they highlight the need to consider the maintenance of these declining areas on a landscape scale.

Keywords : Forest ecosystem, Saproxylic beetle, Dead wood, Tree-related microhabitat, Disturbance ecology, Climate change, Disturbance legacies

Conséquences des dépérissements en forêts tempérées sur les structures d'habitat et la biodiversité

Résumé :

Les perturbations naturelles font partie intégrante des écosystèmes forestiers. Elles assurent la création de nouveaux habitats, maintiennent une forte hétérogénéité spatiale et interrompent les processus de succession écologique. Les écosystèmes forestiers d'une région donnée sont historiquement adaptés aux complexes de perturbations qui affectent cette région (i.e. le régime de perturbation). Ils sont également largement affectés par les perturbations dites anthropiques (e.g. les coupes forestières). Le processus de mort progressive des arbres d'un peuplement forestier, en raison de ces différentes perturbations est appelé « *dépérissement forestier* ». Généralement, ces dépérissements sont suivis de coupes de récupérations ou sanitaires visant à récolter la valeur commerciale des arbres avant leur détérioration ou à endiguer les futures épidémies d'insectes ravageurs. Ces coupes sont considérées comme des perturbations supplémentaires. Toutefois, les changements en cours, tant climatique que d'utilisation des terres, entraînent des modifications du régime de ces perturbations. À l'extrême, si le changement de ces régimes est trop important, il peut conduire à un glissement vers un écosystème non-forestier. Ces changements de régimes pourraient alors entraîner des disparitions régionales d'espèces forestières et altérer les services écosystémiques rendus par les forêts aux sociétés humaines. L'étude de ces dépérissements forestiers apparaît donc d'une importance centrale. Dans le cadre de cette thèse, nous nous concentrons sur la réponse des coléoptères saproxyliques (i.e. les coléoptères liés pour une partie ou totalité de leur cycle de vie, au bois mort), groupe écologique menacé dans les forêts tempérées gérées en raison de la rareté de la ressource bois mort. Nous analysons aussi les changements d'habitats causés par ces dépérissements (i.e. *héritages de perturbation*). Pour cela, nous étudions trois cas d'études de dépérissements européens : (i) la sapinière pyrénéenne (*Abies alba*) et (ii) la chênaie du Val de Loire (*Quercus* spp.) causés par des sécheresses, et (iii) la pessière bavaroise (*Picea abies*) causé par des tempêtes et des épidémies d'*Ips typographus*. Sur chacun de ces sites, nous avons inventorié le bois mort et les dendromicrohabitats présents sur les placettes ainsi que les coléoptères saproxyliques. Ces relevés ont permis de mettre en évidence des changements conséquents d'habitats se traduisant par des augmentations de bois mort et des changements de compositions de dendromicrohabitats. Ces changements sont apparus modulés par la sévérité des dépérissements. En cascade, ces changements d'habitat ont induit des modifications de composition locale des coléoptères saproxyliques. Pour les deux forêts de conifères, les changements d'habitats ont induit des effets positifs du dépérissement sur la diversité locale des coléoptères, tant taxonomique que fonctionnelle. Par ailleurs, nous avons observé des généralisations des communautés de coléoptères saproxyliques dans le paysage en raison du dépérissement. De plus, nous avons mis en évidence l'importance du dépérissement à l'échelle paysagère sur les assemblages taxonomiques, fonctionnelles et phylogénétiques locaux de coléoptères saproxyliques. Nous montrons aussi que les diversités fonctionnelle et phylogénétique ont majoritairement répondu à des processus paysagers. Enfin, nous notons que les coupes sanitaires et de de récupération n'ont pas affecté la diversité locale des coléoptères mais ont fortement altéré leurs relations écologiques. Nos résultats mettent en avant l'intérêt qu'il peut être tiré des zones dépérisantes pour la conservation de groupes d'espèces menacées autrement dans les zones forêts gérées, par le maintien des habitats créés (i.e. bois mort et dendromicrohabitats). Enfin, ils mettent en évidence le besoin de penser le maintien de ces zones dépérisantes par une échelle paysagère.

Mots clés : Ecosystème forestier, Coléoptère saproxylique, Bois mort, Dendromicrohabitat, Ecologie des perturbations, Changement climatique, Héritage de perturbation