# Réponse de la flore, de la faune du sol et de leur substrat à l'introduction d'espèces exotiques envahissantes végétales.

Corentin Abgrall

Normandie Université

# THÈSE

**Pour obtenir le diplôme de doctorat**

**Spécialité SCIENCES DE LA VIE ET DE LA SANTE**

**Préparée au sein de l'Université de Rouen**

# Réponse de la flore, de la faune du sol et de leur substrat à l'introduction d'espèces exotiques envahissantes végétales


**Présentée et soutenue par**
**Corentin ABGRALL**


| **Thèse soutenue publiquement le 17 septembre 2019 devant le jury composé de** | | |
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| M. Grégory MAHY | Professeur,<br>Université de Liège | Rapporteur |
| Mme Annabel PORTE | Directrice de recherche,<br>INRA-UMR Biogeco Bordeaux | Rapporteure |
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**Thèse dirigée par Matthieu CHAUVAT et Estelle FOREY, laboratoire Ecodiv**

UNIVERSITÉ DE ROUEN NORMANDIE

EdNBISE
Ecole doctorale Normande
Biologie Intégrative,
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ECODIV

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# Response of native flora, soil fauna and their habitat to the introduction of invasive alien species


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*« The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' (I've found it!), but 'That's funny...' »*

*-Isaac Asimov.*

## Avant-propos

Cette thèse a été réalisée au sein du laboratoire d'écologie de l'Université de Rouen Normandie – Normandie Université (URA IRSTEA ECODIV) sous la direction du Pr. Matthieu Chauvat et la co-direction du Dr. Estelle Forey-Leyssenne.

Cette thèse a été financée par une allocation doctorale de la région Haute-Normandie (puis Normandie), le LabEx COTE (Université de Bordeaux), d'une bourse de recherche Jean et Marie-Louise Dufrenoy – Crédit Agricole d'Île-de-France Mécénat. Ce projet a également bénéficié d'un soutien de l'Ecole Doctorale Normande - Biologie Intégrétive, Santé, Environnement sous la forme d'une bourse de déplacement pour un colloque international.

Ce manuscrit comprend une introduction générale, quatre chapitres de résultats rédigés sous forme d'articles scientifiques, une discussion générale, une conclusion et des appendices. Ces appendices incluent une publication distincte des travaux de thèse mais fournissant une base méthodologique. Un CV est également présenté en fin de manuscrit.

## Résumé

Les espèces exotiques envahissantes végétales sont des plantes introduites et naturalisées hors de leur aire de répartition native et capables de maintenir et d'accroître leur population. Certaines sont considérées comme transformatrices de par leur effet sur les écosystèmes (structure, fonctionnement ainsi que les communautés végétales et animales). Ces transformations peuvent rendre certaines de ces espèces nuisibles de par leurs impacts écologiques et économiques importants.

Les travaux réalisés dans le cadre de cette thèse et présentés ici ont pour objectif d'approfondir les connaissances sur l'impact des invasions biologiques. La faune du sol, la végétation native et leurs substrats ainsi que son fonctionnement ont été étudiés à différentes échelles spatiales. Deux espèces exotiques, envahissantes en Europe, ont été considérées comme modèles pour ces travaux : le robinier faux-acacia (*Robinia pseudoacacia*) et la renouée du japon (*Reynoutria japonica*).

Premièrement, une méta-analyse globale a permis de démontrer l'effet positif des invasions biologiques végétales sur l'abondance de certains groupes de la faune du sol, notamment les consommateurs primaires, selon la structure de l'habitat (ouvert ou fermé).

Ensuite, une étude à large échelle sur le robinier faux-acacia a permis d'illustrer les différences qui peuvent exister dans la réponse des écosystèmes forestiers aux invasions le long d'un gradient latitudinal. Ce gradient, composé de quatres régions distinctes en Europe de l'Ouest présente des différences de climat et de végétation dominante, ces différences modifiant l'impact du robinier faux-acacia. Une étude appronfondie sur le robinier faux-acacia en Normandie a permis de mieux comprendre son effet sur les communautés animales et végétales ainsi que sur le fonctionnement des écosystèmes par comparaison avec deux essences natives dominantes.

Finalement, une manipulation expérimentale en laboratoire a démontré l'impact des composés allélopathiques de la renouée du Japon sur une partie de la faune du sol. Cette étude a montré que certaines espèces exotiques envahissantes sont susceptibles d'influencer la faune et les réseaux trophiques du sol par leurs métabolites secondaires.

Ces travaux illustrent l'intérêt, dans le contexte des invasions biologiques végétales, de l'étude simultanée des compartiments aériens et souterrains à différentes échelles spatiales.



*Mots-clés :* invasions biologiques, interactions sol-plante, faune du sol, écologie des communautés, robinier faux-acacia, renouée du Japon

## Abstract

Invasive alien plants are species introduced and naturalized outside of their native distribution range and which have the capacity to maintain and expand their population. Some of these species are considered to be ecosystem transformers by altering their structure, functioning as well as resident animal and plant communities. These induced alterations make some of these species undesirable through their ecological and economical impacts.

The work presented in this thesis aims at improving the understanding of the impact of biological invasions by alien plants. The soil fauna, native vegetation and their substrate, as well as ecosystem functioning, were studied at different spatial scales. Two exotic alien species, invasive in Europe, were considered as biological models for this work: the black locust (*Robinia pseudoacacia*) and the Japanese knotweed (*Reynoutria japonica*).

Firstly, a global meta-analysis demonstrated the positive impact that plant invasions exerts on the abundance of some groups within the soil fauna, notably primary consumers, within different types of habitats (open or closed).

Then, a large-scale study on the black locust revealed the differences that occur in the response of forest ecosystems to invasions along a latitudinal gradient. Study sites along this gradient, distributed among four distinct regions in western Europe, exhibit differences in climate and dominant native vegetation which can alter the impact of the black locust. A detailed study on black locust impacts in Normandy demonstrated the impact of *R. pseudoacacia* on native plant and soil fauna communities, as well as on some ecosystem functions, in comparison to two native tree species.

Finally, a laboraty experiment demonstrated the impact that allelopathic compounds extracted from Japanese knotweed rhizomes can have on some organisms within the soil fauna. This study showed that some invasive alient plants can influence the soil fauna, and soil food webs, through their secondary metabolism.

This thesis illustrates that simultaneous study of both aboveground and belowground ecosystem compartments at different spatial scales is of interest in the context of biological invasions.

*Keywords :* biological invasions, soil-plant interactions, soil fauna, community ecology, black locust, Japanese knotweed

## Remerciements

V'là une bonne chose de faite, boudiou ! Une page se tourne… Ça n'a pas été facile tous les jours, et je n'en serais pas arrivé là sans l'aide, le soutien et l'attention d'une belle flopée de personnes. Un grand merci général, donc, à tous ceux qui liront ces quelques lignes et se sentiront concernés.

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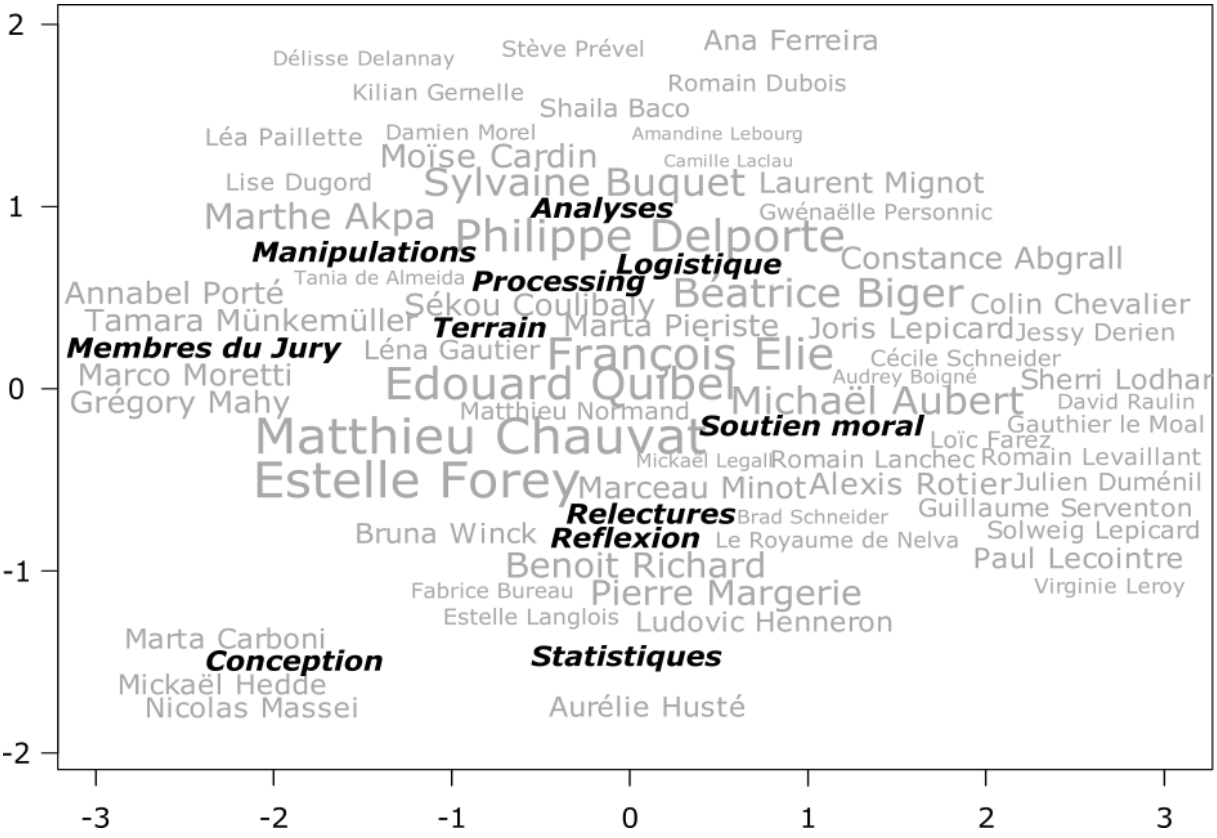

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## Enseignement

En parallèle des travaux de recherche présentés dans le reste du manuscrit cette thèse m'a également donné l'opportunité de m'initier à l'enseignement auprès d'étudiants de licence et de master. Il me parait important de présenter également cet aspect extrêmement intéressant et formateur de la formation doctorale. Ces enseignements ont été dispensés dans le cadre de vacations, d'un contrat de monitorat et d'un contrat d'attaché temporaire d'enseignement et de recherche (A.T.E.R.).

***Master 2 – Gestion de l'Environnement parcours Biodiv***

UE « Milieux Naturels » - 2017/2018 - Encadrement d'une sortie terrain de découverte de la gestion des milieux naturels auprès d'acteurs du domaine dans le Cotentin (20h TD)

***Master 1 – Gestion de l'Environnement parcours Biodiv***

UE « Interaction compartiments épigé-endogé » - 2016/2017 - Développement d'un protocole expérimental d'éthologie entomologique (2h TD), réalisation de l'expérience (4h TP) et analyses statistiques (2h TD). Correction de 7 comptes-rendus.

UE « Interaction compartiments épigé-endogé » - 2017/2018 - Encadrement d'un TP d'identification et de comptage de la faune du sol (macrofaune et mésofaune) (2x3h TP)

***Licence 3 – SVTE parcours Sciences de la Terre***

UE « Exploration et analyses des données environnementales » - 2017/2018 & 2018/2019 - Enseignement des statistiques appliquées au domaine de l'environnement (8x2h TD)

***Licence 3 – SVTE parcours Sciences et Vie de la Terre et Ecologie et Biologie des Organismes***

UE « Ecologie Pratique » - 2017/2018 - Encadrement d'une sortie terrain d'identification des essences forestières, modes de gestion et stades du cycle sylvicole pour réalisation d'une cartographie sous SIG (2x4h TP)

UE « Systématique appliquée » - 2018/2019 – Expérience sur l'effet de la topographie sur les communautés de la macrofaune du sol. Echantillonnage, identification, analyses de données et rédaction d'un rapport (28h TP & 4h TD)

***Licence 3 – SVTE parcours Biologie –Géosciences - Environnement***

UE « Botanique » - 2018/2019 – Comparaison entre grands groupes végétaux avec une attention particulière à l'évolution des caractères reproducteurs au cours du temps et leur implication écologique (46h de TP)

***Licence 1 – Biologie Géosciences (BGC)***

UE « Botanique » - 150 étudiants - 2017/2018 - Encadrement d'un TP sur la diversité morphologique et taxonomique des thallophytes (18x2h TP) et d'un TP sur la morphologie et le rôle fonctionnel des stomates (12x2h TP)

# Introduction générale

Crédit : LightScribe / iStock

**Kudzu (*Pueraria montana var. lobata*)**

# 1. Les espèces exotiques envahissantes : définitions et mécanismes

## *1.1. Définitions*

Le concept d'**espèce exotique** est connu depuis le XIXème siècle et mentionné dans les travaux de plusieurs naturalistes de l'époque tels que Charles Darwin ou Joseph D. Hooker (Richardson & Pyšek, 2007). Les espèces exotiques peuvent être définies comme « des organismes allochtones, ou non-indigènes, introduits hors de leur aire de répartition et de leur potentiel spontané de dispersion » (Richardson *et al.*, 2003). Cette définition sépare ainsi les mécanismes biogéographiques de dispersion spontannée des espèces au cours des temps géologiques des introductions liées aux activités humaines. A cette époque ces espèces sont uniquement considérées comme des curiosités, ou des exemples des mécanismes de dispersion et spéciation (Richardson & Pyšek, 2007). La définition actuelle conseillée, dans le cas des plantes exotiques, est celle suggérée par Richardson *et al.* (2003) : « plantes dont la présence dans une aire donnée est due à une introduction intentionnelle ou accidentelle liée à l'activité humaine. » (Figure 2). Cette définition inclut de manière claire la responsabilité anthropique dans ce phénomène, en tant que vecteur d'introduction.

La définition ci-dessus ne considère pas l'échelle temporelle du phénomène, à savoir la persistance dans le temps de ces espèces dans leur zone d'introduction. Quand ces espèces se maintiennent dans le temps dans leur aire d'introduction grâce à une reproduction spontanée, sans intervention humaine supplémentaire, on parle alors d'**espèces exotiques naturalisées**, ou simplement d'espèces naturalisées (Figure 1 ; Figure 2). L'emprise spatiale de ces espèces peut rester limitée malgré leur naturalisation et n'implique pas nécessairement d'envahissement ultérieur. A noter cependant qu'une période de latence entre la naturalisation et l'envahissement est fréquemment observée (Pyšek & Prach, 1993) et peut aller de 20-30 ans à plus de 40 ans (Aikio *et al.*, 2010).

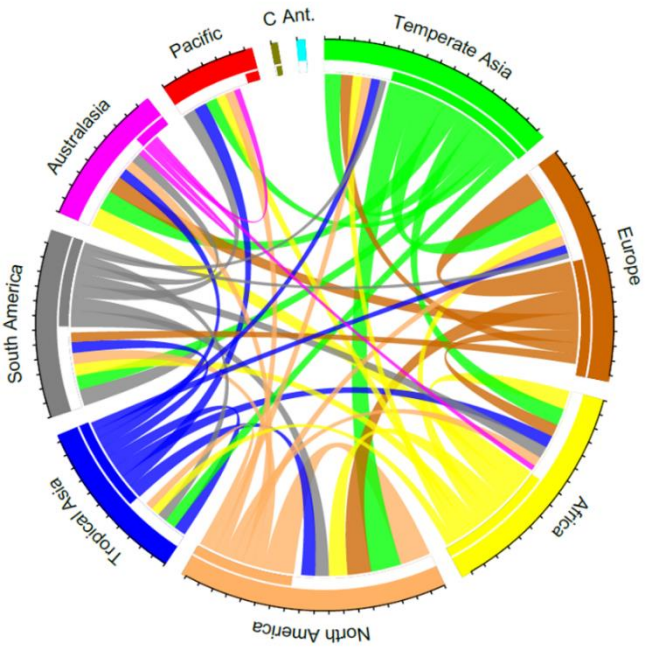



*Figure 1: Flux observés d'espèces de plantes exotiques naturalisées entre continents (représentation pondérée par la taille des continents). Les continents sont ordonnés par importance en tant que source d'espèces. Extrait de van Kleunen et al. (2015) basé sur des données GloNAF.*

Les **espèces nuisibles**, quant à elles, sont des espèces (exotiques ou non) se développant là où elles ne sont pas souhaitées par l'Homme avec des conséquences écologiques et/ou économiques discernables (Figure 2 ; Richardson *et al.*, 2003). Cette définition, fortement anthropocentrée, repose sur une perception humaine subjective de la place des espèces à l'échelle du paysage et des écosystèmes et met l'accent principalement sur les effets économiques. Elle n'oriente pas, en revanche, la nature des conséquences écologiques de la présence de ces espèce. Elle peut également s'appliquer indifféremment à tous types d'espèces indépendamment de leur provenance géographique.

On différencie les **espèces exotiques envahissantes (EEE)** des espèces naturalisées par leur capacité à produire une descendance nombreuse, associée à une capacité de dispersion importante pour cette progéniture (Figure 2 ; Richardson *et al.*, 2003). Là où une espèce naturalisée (hors introductions supplémentaires) restera contrainte spatialement, une espèce exotique envahissante aura la capacité de se disperser spontanément et ainsi de coloniser de nouveaux milieux favorables. Cette définition neutre, en terme d'impact, des EEE s'oppose à la définition alternative et couramment usitée associant capacité de dispersion et impacts négatifs : une EEE est ainsi définie par certaines organisations comme : « une espèce allochtone dont les l'introduction par l'Homme (volontaire ou fortuite), l'implantation et la propagation menacent les écosystèmes, les habitats ou les espèces indigènes avec des conséquences écologiques, économiques ou sanitaires négatives » (UICN, 2000; McNeely & Schutyser, 2003). Cette définition correspond au sens commun d'« **espèce invasive** » par l'implication d'un impact négatif sur les écosystèmes en place (voir partie 3. L'impact des invasions biologiques). De par son anthropocentrisme cette définition semble à proscrire pour y substituer le terme suggéré

**Plantes exotiques :**

Taxons dont la présence dans une aire donnée est due à une introduction intentionnelle ou accidentelle liée à l'activité humaine.

**Plantes naturalisées**

Espèces exotiques capables de reproduction spontanée, et de maintien de populations dans le temps, dans leur aire d'introduction sans intervention humaine supplémentaire.

**Plantes exotiques envahissantes**

Espèces exotique naturalisées produisant une descendance fertile, généralement en nombre considérable, et capable d'une dispersion importante permettant la colonisation d'une aire importante.

**Plantes nuisibles**

Plantes, exotiques ou non, se développant sur des sites où elles ne sont pas souhaitées avec des conséquences écologiques et/ou économiques détectables.

**Plantes transformatrices**

Sous-ensemble des espèces exotiques envahissantes modifiant la structure, le fonctionnement et/ou la nature d'un écosystème et ce sur une surface proportionnellement importante relative à cet écosystème.

**Invasions biologiques**

Accroissement durable de l'aire de répartition d'un taxon à l'échelle d'une période géologique ou paléontologique identifiable.

*Figure 2: Terminologie recommandée par Richardson et al. (2003) et Williamson et al. (1996) dans le champ disciplinaire des invasions biologiques végétales*

par Richardson *et al.* (2003), celui d'**espèces transformatrices**. Ces espèces sont définies comme un sous-ensemble au sein des EEE dont la présence entraîne des modifications au sein de la structure, du fonctionnement et/ou des charactéristiques de l'écosystème et ce sur une surface importante relativement à la taille de cet écosystème. Cette définition intègre donc la notion d'EEE à celle d'espèce nuisible, sans l'anthropocentrisme de la « présence non désirée » d'une espèce ou l'aspect négatif de leur effet.

Le terme « **invasion** », quant à lui, a été utilisé pour la première fois dans le sens biologique par Goeze en 1882 dans son ouvrage *Pflanzen-geographie* en relation avec la propagation d'espèces exotiques, ou non-natives. Cette définition désigne alors uniquement les espèces introduites hors de leur aire de répartition et se propageant de manière importante, et ne caractérise alors que l'aspect spatial et temporel du phénomène sans lien avec leur impact potentiel, positif ou négatif (Rejmanek *et al.*, 2002). Néanmoins l'usage même du terme « invasion », issu du vocabulaire martial, donne implicitement une connotation négative au phénomène.

La publication faisant référence en tant que fondement de l'étude des invasions biologiques est le traité publié en 1958 par Charles Elton, *The Ecology of Invasions by Plant and Animals* (Elton, 1958). Dans cet ouvrage, Elton redéfinie des concepts d'écologie générale et évolutive dans le contexte des invasions biologiques, présente de nombreux cas d'étude à l'échelle planétaire, identifie les vecteurs relatifs à ce phénomène puis finit par suggérer divers mécanismes susceptibles sous-jacents aux invasions biologiques. Cette publication, en revanche, ne définit pas les termes « d'invasion » ou « d'envahisseur ». La définition de référence dans le domaine scientifique est celle donnée par Williamson dans son ouvrage *Biological Invasions* en 1996 qui définit les invasions biologiques comme: « l'accroissement durable de l'aire de répartition d'un taxon sur une période identifiable à l'échelle géologique ou paléontologique ».

### *1.2. Les mécanismes de transition vers l'envahissement*

La capacité pour une espèce exotique de se naturaliser, de devenir envahissante repose, selon le cadre conceptuel défini par Richardson *et al.* (2003), sur la capacité de ces dernières à s'affranchir d'un ensemble de filtres géographiques, environnementaux ainsi que dispersifs et reproducteurs (Figure 3). Le franchissement du **filtre géographique** (Figure 3-1) est propre à l'historique même des espèces exotiques : elles sont allochtones. Ce filtre peut être intercontinental ou intracontinental mais implique un déplacement plus important que celui permis par les capacités intrinsèques de dispersion de l'espèce. Le **filtre environnemental local** (Figure 3-2) peut-être abiotique (*e.g.* climatique) ou biotique (*e.g.* pathogènes) et représente la capacité de l'espèce exotique à survivre dans les conditions du milieu où elle s'est trouvée introduite. Le **filtre reproductif** (Figure 3-3) sélectionne les espèces exotiques capables de se reproduire dans les conditions du milieu où elles ont été introduites (Figure 3-2) mais aussi de maintenir cette capacité, et leur population, dans le temps (Figure 3-c). Comme défini précédemment on parle alors d'espèces exotiques naturalisées. Le **filtre dispersif** (Figure 3-4) sélectionne les espèces capables à la fois de maintenir leur population mais également de l'accroître grâce à une dispersion importante : et donc de devenir envahissantes (Figure 3-d). Le franchissement de ce filtre diffère selon la modalité de dispersion (plus de 100 m en moins de 50 ans pour les taxons se propageant par graines ou propagules et plus de 6 m en moins de 3 ans pour les espèces stolonifères ou rhizomateuses). Les deux derniers **filtres environnementaux du milieu** (Figure 3-5,6) séparent les espèces exotiques envahissantes exploitant une perturbation préalable de l'écosystème pour s'installer (Figure 3-e) des espèces capables de s'installer dans des habitats naturels en déplaçant les espèces natives (Figure 3-f). La capacité de ces espèces exotiques envahissantes à affecter le fonctionnement et/ou la structure des écosystèmes peut, selon les définitions, être nécessaire pour qu'elles soient considérées comme envahissantes ou les placer dans la catégorie des EEE « transformatrices ».

Une règle empirique concernant la transition des espèces exotiques vers la naturalisation et l'envahissement est la « Règle des 10 % » qui postule que 10 % des espèces importées s'échappent de leur lieu d'introduction et persistent transitoirement dans la zone d'introduction, 10 % de ces espèces deviennent naturalisées et 10% des espèces exotiques naturalisées deviennent envahissantes (Pyšek *et al.*, 2004; Richardson & Pyšek, 2006). Cette règle souffre de nombreuses exceptions, limites et réserves mais reste applicable comme référence et étalon de l'avenir des espèces exotiques. La carte présentée en Figure 4 présente une évaluation des risques d'invasions biologiques (c.-à-d. naturalisation et envahissement) pour le XXI$^{ème}$ siècle.

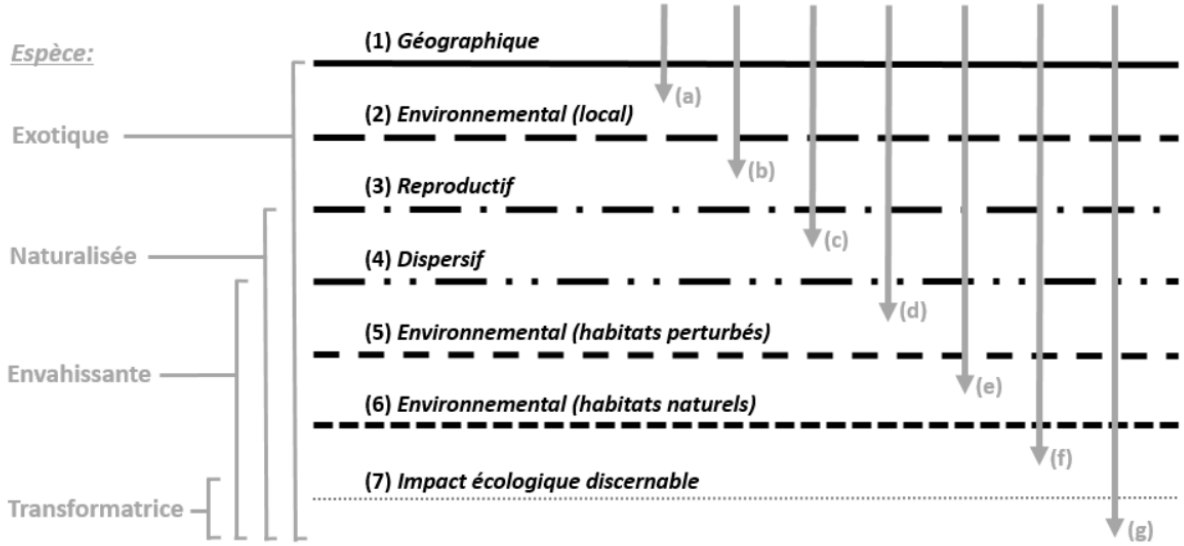



*Figure 3: Représentation schématique des filtres écologiques et pratiques limitant la propagation des espèces exotiques et représentation de la terminologie associée pour nommer les espèces. (1-6) filtres écologiques, (7) répercussions environnementale, (a-g) Chemin suivi par des taxons pour arriver à différent statuts. Adapté de Richardson et al. (2003).*

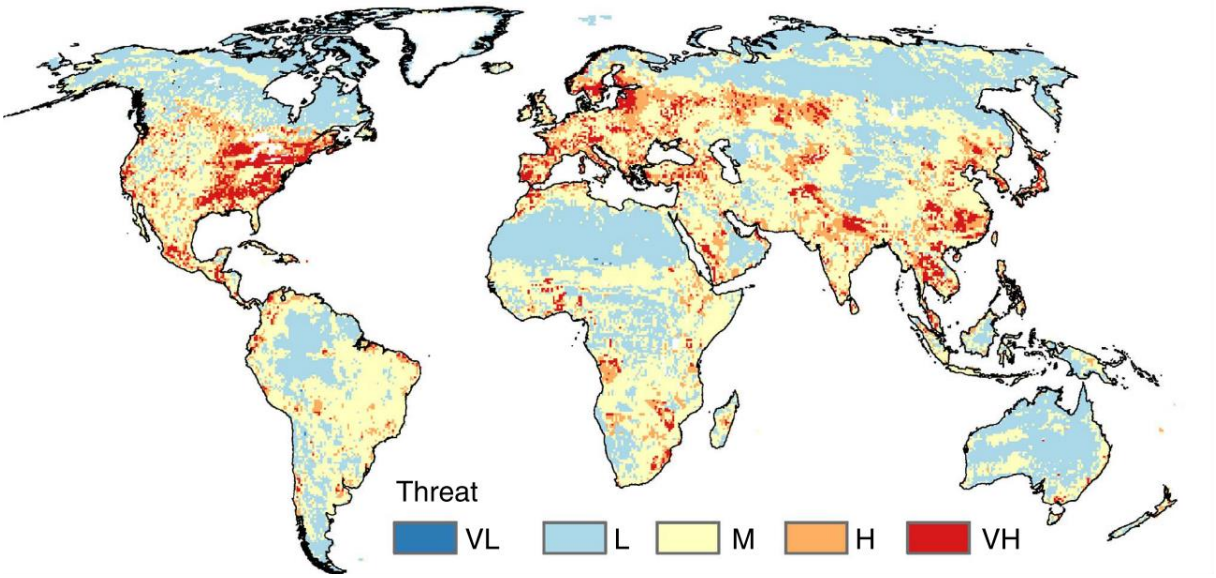



*Figure 4: Risques globaux d'invasions biologiques au XXI$^{ème}$ siècle. Prend en compte la capacité portuaire et aéroportuaire, les importations animales et végétales entre 2000 et 2009 pour évaluer le risque global d'introduction. Les déplacements prédits de biomes, l'augmentation de l'intensité de l'activité agricole et le risque accru d'incendie sont combinés pour évaluer le risque de d'envahissement par les espèces exotiques. Le risque d'introduction et d'envahissement sont agrégés dans la carte ci-dessus évaluant les risques globaux. VL : risque très faible, L : risque faible, M : risque moyen, H : risque élevé VH : risque très élevé. Extrait de Early et al. (2016).*

Les hypothèses, et mécanismes associés, expliquant la capacité d'une espèce exotique à faire la transition entre naturalisation et envahissement, et à devenir transformatrice, sont nombreux (Table 1). La plupart de ces mécanismes sont complémentaires les uns avec les autres, voire redondants, et ont pour la majorité été démontrés dans des études de cas. La généralisation est en revanche plus complexe, les causes de la transition vers l'envahissement étant généralement multifactorielles. Quelques grandes généralités peuvent en revanche être extraites de la littérature.

Les perturbations du milieu sont une des causes prépondérantes pouvant expliquer l'envahissement par les espèces exotiques, en relation avec la diversité des communautés natives, une diversité faible pouvant être une cause ou une conséquence des invasions biologiques (Levine & D'Antonio, 1999; Chabrerie *et al.*, 2008). Il s'agit d'une des hypothèses les plus anciennes expliquant les invasions biologiques, basée sur les travaux d'Elton (1958) et la théorie de l'évolution (Darwin, 1859). Les niches vacantes dans des écosystèmes peu diversifiées (Table 1-11), ou dont la diversité a été négativement affectée par une perturbation (Table 1-5,9), constituent des opportunités d'établissement pour les EEE. Alternativement les perturbations peuvent être directement responsables de l'invasion en permettant aux EEE (à grande capacité de dispersion et croissance rapide) de se développer rapidement (Table 1-10) tout en affectant les communautés natives. La diversité des communautés locales peut aussi être directement affectée négativement par exclusions compétitive comme *conséquence* des invasions biologiques, sans intervenir causalement dans l'envahissement (Table 1-8).

Le temps de résidence (c.-à-d. la durée depuis l'introduction ; Table 1-14) est un facteur prépondérant dans la détermination de l'invasibilité (c.-à-d. propension à l'envahissement) d'une espèce exotique naturalisée (Rejmánek, 2000). Les espèces exotiques récemment introduites ont généralement un temps minimum de résidence moyen significativement moindre que celui des espèce naturalisée, lui-même inférieur à celui des espèces envahissantes (Pysek & Jarosik, 2005). Ceci peut-être lié à une pression de propagules accrue avec le temps (Table 1-13), à l'évolution dans la zone d'introduction d'aptitudes compétitives accrues (Table 1-7), à un auto-renforcement de l'invasion (effet « cascade » ; Table 1-14) ou même la coévolution d'un mutualisme renforcé (Table 1-12).

*Table 1: Exemples de théories mécanistiques relatives à l'implantation d'espèces exotiques végétales et à leur capacité à devenir envahissantes et/ou transformatrices. Extrait de Richardson et Pyšek (2006), Catford et al. (2009) et Gurevitch et al. (2011).*

| *Hypothèse* | *Définition* | *Références* |
|---|---|---|
| **1. Traits originaux** | Les espèces exotiques envahissantes possèdent des traits originaux sans équivalents fonctionnels dans les écosystèmes envahis. | (Atallah *et al.*, 2014; Macel *et al.*, 2014) |
| **2. Armes novatrices** | Les espèces exotiques envahissantes possèdent des métabolites secondaires allélopathiques non présents dans l'écosystème envahi et contre lesquelles les espèces natives n'ont pas de défense. | (Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004) |
| **3. Préadaptation** | Succès accru des espèces exotiques provenant de régions floristiques diversifiées phylogénétiquement et fonctionnellement où la compétition est forte. | (Mack, 2012; Fridley & Sax, 2014) |
| **4. Propension à l'invasivité des espèces exotiques** | Certaines espèces exotiques sont plus susceptibles que les autres de devenir envahissantes de par leurs traits, leur phylogénie, leur temps de résidence, leurs mutations dans leur aire allochtone, etc. | (Alpert *et al.*, 2000; Richardson & Pyšek, 2006; Van Kleunen *et al.*, 2010a) |
| **5. Invasibilité des communautés ou habitats** | Certain(e)s communautés, habitats, écosystèmes et régions sont plus propices à l'envahissement que d'autres, de par la pression d'apport en espèces invasives, ou leur résistance inhérente. | (Alpert *et al.*, 2000; Richardson & Pyšek, 2006) |
| **6. Libération des ennemis naturels** | Les espèces exotiques envahissantes ne sont plus contraintes, dans leur aire d'introduction, par les prédateurs et pathogènes avec lesquelles elles ont co-évolué. | (Keane & Crawley, 2002) |
| **7. Evolution d'aptitudes compétitives accrue** | En l'absence d'herbivores la sélection favorise les génotypes allouant des ressources plus importantes à l'aptitude compétitive (croissance végétative et reproduction) qu'à la défense contre les herbivores. | (Blossey & Notzold, 1995) |
| **8. Modèle 'pilote'** | Une perturbation externe permet l'invasion biologique qui elle-même ultérieurement entraine une diminution locale de biodiversité par exclusion compétitive. | (Chabrerie *et al.*, 2008) |
| **9. Modèle 'opportuniste'** | Perturbation externe du milieu occasionnant une perte locale de diversité fragilisant l'écosystème et permettant l'invasion. | (Chabrerie *et al.*, 2008; White *et al.*, 2013) |
| **10. Modèle 'passager'** | Les espèces exotiques envahissantes possèdent des capacités de dispersion supérieure à celles des espèces natives importante leur permettant de « préempter » l'espace en cas de perturbation. | (Turkington & MacDougall, 2005; Chabrerie *et al.*, 2008) |
| **11. Résistance et niches écologiques vides** | Résistance accrue des communautés diverses aux invasions par l'absence de niches fonctionnelles vides. | (Levine & D'Antonio, 1999; Stachowicz & Tilman, 2005) |
| **12. Mutualisme renforcé** | Effet plus positif des organismes mutualistes dans l'aire d'envahissement que dans l'aire native sans changement d'effet des antagonistes. | (Marler *et al.*, 1999; Reinhart & Callaway, 2006; Sun & He, 2010) |
| **13. Pression des propagules** | Influence forte de la taille, du nombre et de la périodicité de la production des propagules sur la probabilité de survie et de dispersion des espèces exotiques leur permettant de devenir envahissantes | (Colautti *et al.*, 2006; Simberloff, 2009) |
| **14. Effondrement et effet cascade** | Des interactions positives entre EEE transformatrices peuvent initier des rétroactions positives au niveau de la population intensifiant les impacts et favorisant des invasions secondaires. | (Simberloff & Holle, 1999; Green *et al.*, 2011; Yelenik & D'Antonio, 2013) |
| **15. Temps minimal de résidence** | La transition entre la naturalisation et l'envahissement est fonction du temps (minimum) de résidence de l'espèce dans l'écosystème. | (Rejmánek, 2000; Pysek & Jarosik, 2005) |

L'envahissement peut également être dû à des cause intrinsèques propres à chaque espèce, liées à leurs traits (Grotkopp & Rejmánek, 2007; Dawson *et al.*, 2011), et constituant une « propension à l'invasivité » de chaque espèce (Table 1-4). Les EEE, de par leur origine allochtone et leur histoire évolutive distincte, possèdent fréquemment des traits originaux non présents dans l'écosystème envahi (Table 1-1). Ces traits peuvent être morphologiques, physiologiques ou biochimiques (c.-à-d. allélopathie ; Table 1-2). Les espèces ayant évolué dans des régions biogéographiques diversifiées (où la compétition interspécifique est importante) et introduites dans des zones moins diverses et compétitives comme les îles, peuvent également posséder une « préadaptation » à la compétition interspécifique plus importante que celles des espèces natives (Table 1-3). Cette observation s'applique également, de manière inverse, à l'échappement aux prédateurs et pathogènes naturels avec lesquelles l'espèce a coévolué, et la contraignant dans sa dispersion et sa compétitivité dans son aire de répartition native (Table 1-6).

Les causes de l'envahissement par les espèces exotiques naturalisées (c.-à-d. invasions biologiques) sont donc diverses et peuvent être liées à des facteurs intrinsèques (traits, histoire évolutive, etc) ou extrinsèques (diversité locale, contraintes climatiques, etc) aux EEE.

## 2. Les sols et leur biocénose

Les travaux présentés dans ce manuscrit accordent une place importante à la réponse des organismes vivants dans le sol à la présence d'espèces exotiques envahissantes et transformatrices. Beaucoup de ces organismes sont mal connus et méritent d'être présentés ici. Les sols sont l'un des habitats les plus complexes et pourtant parmi les moins étudiés, notamment au vu de la difficulté relative de prospection et d'étude de ces milieux. Les communautés biologiques occupant ce milieu font partie des plus diversifiées tant phylogénétiquement (25 % des 1,5 millions d'espèces décrites ; Decaëns, 2010), que morphologiquement [de quelques µm (microfaune) à plusieurs dizaines de cm (macrofaune et mégafaune) ; Figure 6 ; Swift *et al.*, 1979] et fonctionnellement (participations à de nombreux processus écologiques : cycles biogéochimiques, pédogénèse, régulation des populations, etc). Ces organismes édaphiques sont impliqués dans un nombre important de processus écologiques fournissant ainsi un ensemble de services écosystémiques clés pour les populations humaines (Lavelle *et al.*, 2006).

Le compartiment sol (endogé), et les organismes qui y résident, ont reçu une attention relativement moindre en comparaison à celle accordée aux compartiments aériens (épigés) dans le contexte des invasions biologiques (Wolfe & Klironomos, 2005; Litt *et al.*, 2014). Les écosystèmes terrestres sont néanmoins composés de compartiments épigés et endogés interagissant de manière complexe et multifactorielle (Figure 5 ; Wardle *et al.*, 2004). Ces interactions jouent un rôle important dans la régulation du fonctionnement des écosystèmes (Coleman, 2008) et sont susceptibles d'être affectées de nombreuses manières, directes (*e.g.* allélopathie, remplacement de la source d'alimentation, etc), comme indirecte (*e.g.* modification de l'habitat, altération de la quantité et de la quantité de la litières, etc) par les invasions biologiques végétales.

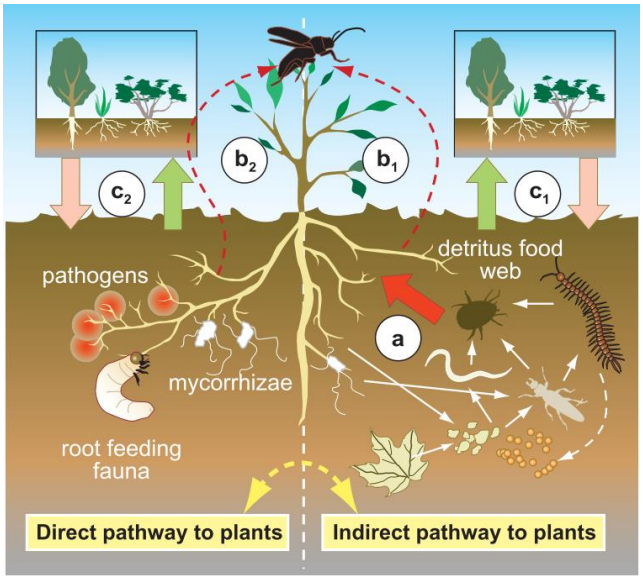



*Figure 5: Schéma représentant les interactions entre organismes endogés et les plantes et mettant en avant les rétroactions des organismes du sol sur les plantes. Liens directs (gauche) : certains organismes édaphiques exercent un effet direct sur les plantes en consommant les racines ou en formant des relations antagonistes (*e.g. *parasitisme) ou mutualistes (*e.g. *mycorrhizes) avec leur plante-hôte. Ces relations influencent directement les plantes mais également les organismes les consommant ($b_2$) et, potentiellement, leurs prédateurs. Liens indirects (droite) : la consommation de détritus (végétaux ou animaux) par de nombreux organismes du sols (*i.e. *détritivores) favorise l'acquisition de nutriments par les plantes en (a) en stimulant le recyclage des nutriments et influençant ainsi indirectement les herbivores épigés ($b_1$). Extrait de Wardle* et al *(2004).*

La Figure 6, extraite de Decaëns (2010), présente de manière non exhaustive les principaux groupes d'organismes présents dans les sols en fonction de leur taille et présente (par code couleur) les groupes considérés dans le cadre de ce travail et le niveau de détail de leur identification systématique ou fonctionnelle.

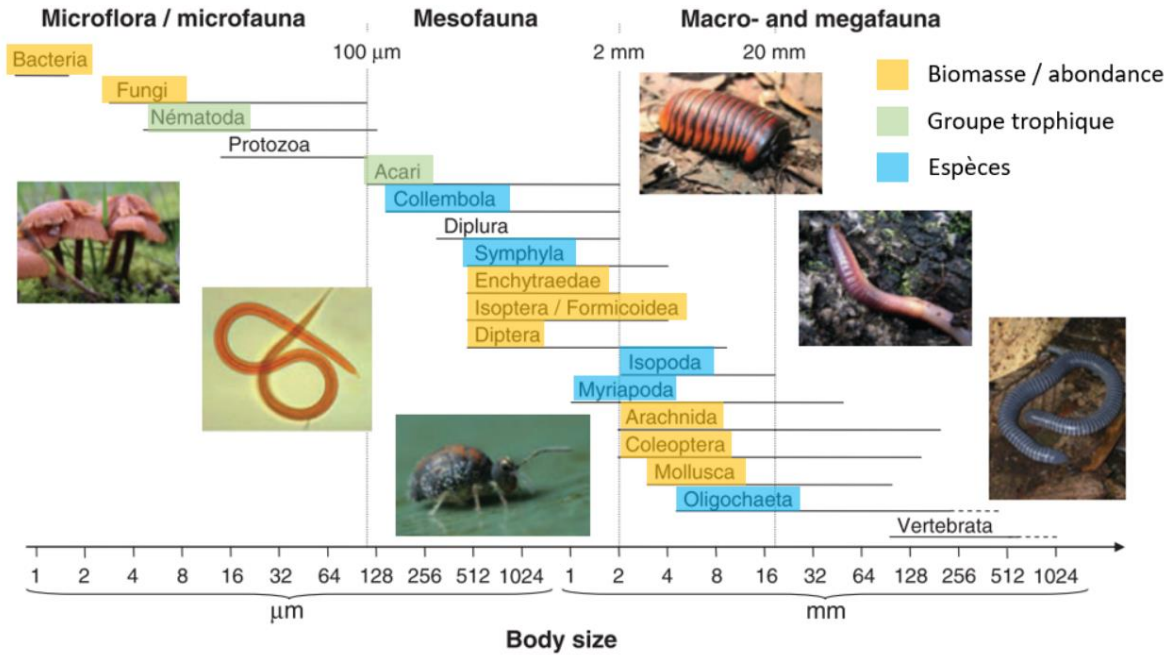



*Figure 6: Principaux groupes d'organismes du sol en fonction de la taille (longueur) de leur corps. Les couleurs indiquent le niveau de détail (c.-à-d. résolution taxonomique) de la prise en compte de ces taxons dans le cadre de ce travail, peut varier suivant expériences et chapitres. Adapté de Decaëns (2010) d'après Swift et al. (1979).*

### *2.1. La microflore/microfaune*

La microflore du sol est constituée principalement de deux grands groupes d'organismes: les bactéries et les champignons. Ces microorganismes peuvent être subdivisés en trois grands groupes trophiques : saprotrophes (dégradant la matière organique morte), mycorrhiziens (champignons formant des associations symbiotiques racinaires avec les végétaux) et parasites (organismes impliqués dans une relation trophique antagonistes avec leur hôte). Certaines bactéries, principalement du genre *Rhizobium,* peuvent également former des symbioses avec les racines de nombreuses plantes, notamment les Fabacées, dans des structures racinaires appelées nodosités. Ces symbioses permettent aux plantes eucaryotes de fixer l'azote atmosphérique ($N_2$) grâce à une enzyme, la nitrogénase, produite par le partenaire bactérien. Le partenaire végétal fournit en contrepartie des glucides et autres substances organiques nécessaire au partenaire bactérien.

La microflore saprotrophe assure la dégradation et la minéralisation de la matière organique, fréquemment après fragmentation par la méso- et macrofaune. Les bactéries saprotrophes dégradent préférentiellement la matière organique labile (facilement décomposable) tandis que les champignons

saprotrophes, grâce à un arsenal enzymatique plus développé, vont pouvoir dégrader la matière organique plus récalcitrante notamment certaines macromolécules polymérisées telles que la lignine (Coleman *et al.*, 2004). En modifiant la qualité et la quantité de l'apport en matière organique détritique (Ashton *et al.*, 2005; Prescott & Zukswert, 2016), en remplaçant les espèces végétales natives (Hejda *et al.*, 2009), les plantes exotiques envahissantes sont susceptibles d'affecter de manière importante les communautés de la microflore. Ces organismes représentant une source importante de ressource trophique pour beaucoup d'autres organismes du sol (Figure 7), une réponse de leur part peut avoir des répercussions sur les maillons supérieurs des réseaux trophiques (effet « bottom-up »).

La microfaune comprend certains animaux de taille inférieure à 0,1 mm tels que les nématodes, les tardigrades ou les rotifères (Figure 6) ainsi que les protozoaires. Ces organismes, ne pouvant creuser le sol eux-mêmes, vivent dans la porosité du sol et l'eau interstitielle qu'elles contient. Les nématodes constituent un embranchement de vers non segmentés classés parmi les ecdysozoaires. Il s'agit d'un groupe très étudié dans la littérature, présents dans tous types de milieux, et très diversifiés notamment en terme de régime trophique (Figure 7 ; Morriën *et al.*, 2012; Yeates *et al.*, 1993). On peut ainsi trouver parmi les nématodes de consommateurs de microflore (bactérivores et fongivores), des phytoparasites ou herbivores racinaires, des parasites ainsi que des prédateurs et des omnivores. Ces différents groupes trophiques sont discernables par observation des pièces buccales au microscope et leur extraction du sol peut se faire relativement facilement et rapidement par l'utilisation de la méthode de Baermann, méthode reposant sur l'hygrotropisme positif et le thermotropisme négatif de ces organismes (McSorley & Walter, 1991). Cette diversité, et la facilité relative d'extraction et d'identification des groupes trophiques, les rend très utiles comme outil d'étude des modifications induites au sein des réseaux trophiques du sol., notamment par une perturbation ou un stress extérieur tel que les invasions biologiques.

### *2.2. La mésofaune*

La mésofaune est composée des espèces dont la taille est comprise entre 0,1 et 2,0 mm (Figure 6). Elle inclue divers microarthropodes communs et abondants (Acariens, Collemboles) ou plus rares (Diploures, Protoures). Ce groupe d'organisme inclue également certains représentants de petites taille de groupes appartenant à la macrofaune (voir 2.3) tels que les pseudoscorpions (Arachnides), symphyles (Myriapodes), enchytréides (Annélides) ou encore certains taxons parmi les fourmis (Formicidés). Ces organismes peuvent présenter différents régimes trophiques (Figure 7). Beaucoup consomment la microflore et la microfaune (par exemple certains collemboles et acariens consomment des nématodes ; Chamberlain *et al.*, 2006), d'autres consomment des détritus végétaux

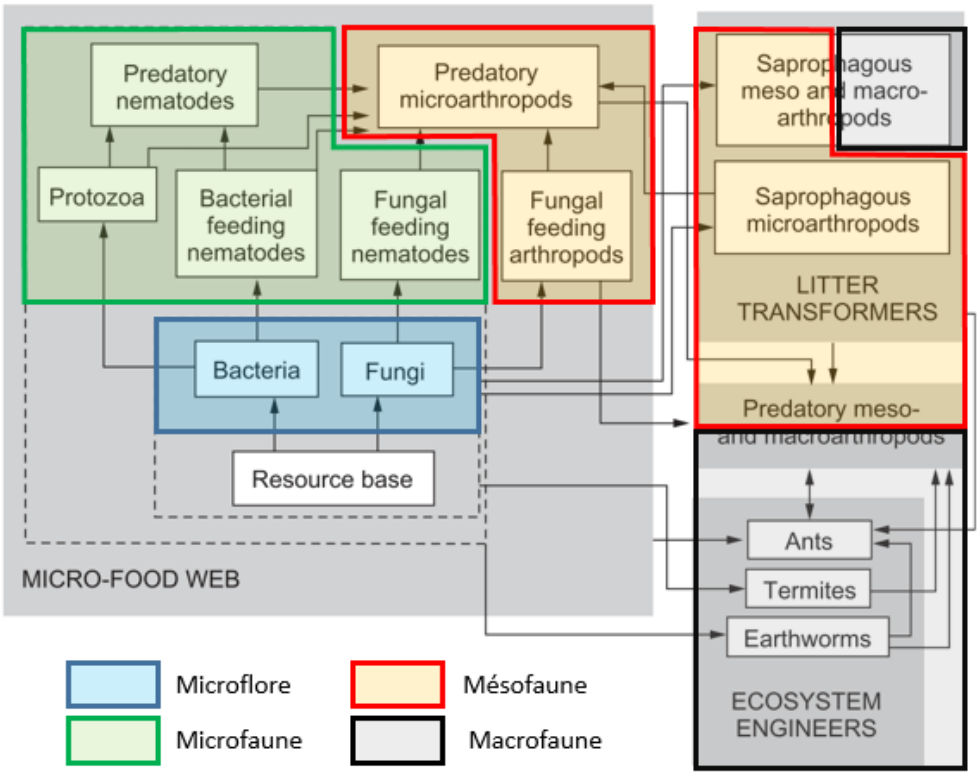



*Figure 7: Organisation schématique des réseaux trophiques du sol. « Micro-food-web » : réseau trophique microscopique, « Litter transformers » : transformateurs de litière, « Ecosystem engineers » : ingénieurs des écosystèmes. Adapté de Coleman et al. (2004) ; d'après Wardle (2002).*

ou les racines fines des plantes (Endlweber *et al.*, 2009). Par leur alimentation ils peuvent affecter les processus de recyclage de la matière organique et ainsi interagir directement ou indirectement avec la végétation (Brussaard, 1998; Wardle *et al.*, 2004a) et sont susceptibles d'être affectés par des modifications au sein des communautés de la microflore et de la microfaune (Scheu & Simmerling, 2004; Sauvadet *et al.*, 2017). De par leur petite taille ils sont également des proies fréquentes de nombreux organismes au sein de la macrofaune (voir 2.3) tels les araignées, les coléoptères ou les centipèdes (Scheu & Falca, 2000). Vivant directement en contact avec le sol, un milieu fortement tamponné (Morecroft *et al.*, 1998) ils sont généralement sensibles aux modifications biotiques comme abiotiques de leur environnement. Leur statut intermédiaire au sein des réseaux trophiques du sol, ainsi que leur sensibilité aux modifications de leur habitat, permet à l'étude de ces organismes d'appréhender d'éventuelles perturbations au sein de ces réseaux et dans les fonctions en dépendant (Coleman, 2008).

### 2.3. La macrofaune et la mégafaune

La macrofaune est composée des espèces dont les individus ont une taille comprise entre 2 et 20 mm. La mégafaune, elle, comprend les organismes de taille supérieure à 20 mm mais, par volonté de simplification, les deux sont fréquemment amalgamés notamment pour les invertébrés tels que les

lombrics. Ces groupes incluent de nombreux insectes (*e.g.* fourmis, coléoptères) ou leurs larves (*e.g.* diptères, coléoptères), des myriapodes (Diplopodes et Chilopodes), cloportes (Isopodes) ou encore les lombrics. Certains, comme les fourmis, lombrics et termites sont des « ingénieurs d'écosystème » (Figure 7), altérant la structure physique du sol et influençant les flux d'énergie et transferts de nutriments (Coleman *et al.*, 2004). Ils participent ainsi à la fragmentation de la matière organique et à son incorporation dans le sol (Clause *et al.*, 2014), consomment d'autres organismes au sein de la faune du sol (Scheu & Falca, 2000) appliquant ainsi une régulation « top-down » aux réseaux trophiques du sol (Viketoft & van der Putten, 2015), structurent le sol de par leur activité (Bhadauria & Saxena, 2009; Clause *et al.*, 2014). En tant que consommateurs de matière organique d'origine végétale, vivante ou morte, ils peuvent être fortement impactés par des modifications au sein des communautés végétales épigées.

## 3. L'impact des invasions biologiques végétales

L'introduction d'espèces exotiques envahissantes a reçu une attention de plus en plus importante ces dernières décennies de la part de la communauté scientifique (*e.g.* Lockwoord *et al.*, 2007; Richardson, 2011) et des acteurs publics internationaux (e.g. Millenium ecosystem assessment, 2005; Delivering Alien Invasive Species Inventories for Europe (DAISIE), 2008). Cette prise d'intérêt est liée à la gravité des effets négatifs de plus en plus prégnante avec le temps (Lockwoord *et al.*, 2007), à l'auto-renforcement des invasions biologiques (Yelenik & D'Antonio, 2013), et à l'augmentation du nombre d'espèces déplacées hors de leur aire native (Simberloff *et al.*, 2013). Le nombre de publications n'a cessé de croître depuis cette période (Richardson, 2011) renforçant d'autant la compréhension du sujet. Les biais géographiques et taxonomiques son nombreux dans le domaine des invasions biologiques avec une surreprésentation de certaines aires géographiques (*e.g.* Europe, Amérique du Nord) et de certains groupes d'organismes invasifs en fonction de leur impact passé plus que potentiel (Pyšek *et al.*, 2008).

Les effets des invasions biologiques végétale sont multifactoriels et peuvent différer selon les compartiments considérés. Un impact négatif sur un compartiment d'un écosystème peut avoir des répercussions considérées comme positives sur d'autres compartiments. Les effets les mieux décris concernent ceux sur la biodiversité native végétale.

### *3.1. Sur la flore native*

Les plantes exotiques envahissantes, de par leur nature, dispersent abondamment et occupent l'espace disponible dans les habitats envahis. Les impacts les mieux connus concernent ainsi les répercussions sur la végétation native (*e.g.* Hejda *et al.* 2009, Vilà *et al.* 2011, Pyšek *et al.* 2012) au vu de la visibilité du remplacement des espèces natives par l'espèce allochtone. Beaucoup d'études ont étudié uniquement l'effet sur la richesse spécifique sans prendre en compte la diversité et l'équitabilité au sein des communautés végétales, masquant une partie de l'effet potentiel (Hejda *et al.*, 2009).

De nombreuses études ont montré des diminutions drastiques de la diversité végétale dans les zones largement envahies par des plantes introduites (Powell *et al.*, 2011) aboutissant à la conclusion que les espèces exotiques envahissantes constituent l'une des menaces majeures pesant sur la biodiversité, avec les changements d'usage des sols et climatiques (UICN, 2000). Les échanges d'espèces entre continents et régions biogéographiques (Figure 1) tendent à causer une homogénéisation de la flore à l'échelle des paysages ou des régions biogéographiques (Lockwoord *et al.*, 2007) malgré une augmentation possible de la diversité végétale via les introductions (Winter *et al.*, 2002). Les observations d'extinctions d'espèces végétales natives causées par des plantes

exotiques envahissantes sont relativement rares à l'heure actuelle (Sax & Gaines, 2008). Elles pourraient en revanche s'accroitre drastiquement dans le futur en fonction des répercussions sur le long terme des changements climatiques (Sax & Gaines, 2008) et futurs (Dukes & Mooney, 1999; Early *et al.*, 2016). Les perspectives biogéographiques permettent d'appréhender les patrons globaux mais peuvent ne pas refléter l'impact local des invasions biologiques sur les communautés et les habitats. Les prédicteurs du succès de l'envahissement peuvent ainsi varier fortement en fonction de l'échelle spatiale considérée (Carboni *et al.*, 2015). Les impacts sur les communautés végétales par suppression des espèces natives sont généralement le reflet de la prise de dominance de l'EEE (Hejda & Pyšek, 2006; Tererai *et al.*, 2013) qui peut avoir des raisons multiples malgré leur finalité similaire (mais voir Pyšek *et al.* 2012).

L'intensité des impacts des invasions biologiques à l'échelle des communautés sont fonction du niveau de dominance des EEE au sein de ces mêmes communautés. Un certain nombre de traits ont été considérés comme bons prédicteurs du risque d'envahissement pour une espèce exotique et reflètent généralement une aptitude compétitive supérieure (Davidson *et al.*, 2011). Quelques exemples de ces prédicteurs sont le taux de croissance des plantules (Grotkopp & Rejmánek, 2007), une aptitude forte à la compétition pour la lumière (c.-à-d. surface spécifique foliaire élevée ; (Grotkopp & Rejmánek, 2007), la hauteur maximale ou encore la couverture de la canopée (Hejda *et al.*, 2009). Plus que les valeurs absolues de ces traits la dissimilarité fonctionnelle et phylogénétique avec les espèces natives présentes dans la communauté semble cruciale (Carboni *et al.*, 2015). Ces considérations reflètent à la fois les mécanismes d'envahissement et leurs impacts, les deux étant difficiles à décorréler dans le cas de l'impact sur les communautés végétales natives. Comme présenté par Chabrerie *et al.* (2008), la diminution de la diversité native peut-être la conséquence ou la cause d'une invasion biologique en réponse à une perturbation du milieu. Les deux peuvent également être concomitantes à la perturbation.

Les EEE bénéficient également fréquemment d'une efficience accrue dans leur utilisation des ressources nutritives (Funk & Vitousek, 2007) et profitent donc fortement d'une disponibilité accrue en nutriments, plus que les essences natives (Blumenthal *et al.*, 2009). Il s'agit d'une exclusion compétitive des espèces natives. Alternativement, certaines EEE notamment ligneuses peuvent enrichir le milieux en nutriments (Vitousek & Walker, 1989) et affecter négativement les espèces natives oligotrophes par une eutrophisation du milieu. Dans les milieux dépendants d'incendies périodiques la dominance d'une EEE peut altérer les régimes de feu par modification de l'inflammabilité de l'écosystème (en l'augmentant ou, au contraire, la diminuant) avec de possibles rétroactions positives pour l'invasive, et négatives pour les espèces natives (Brooks *et al.*, 2006).

Les EEE subissent généralement une pression d'herbivorie moindre que les espèces natives (Procheş *et al.*, 2008; Hartley *et al.*, 2010) et inférieure à celle qu'elles même subissent dans leur aire de répartition native (Keane & Crawley, 2002; Maurel *et al.*, 2013). On observe fréquemment une préférence trophique envers les espèces natives par les herbivores du milieu (Procheş *et al.*, 2008). Ceci aboutit à une pression plus importante sur les espèces natives, donc une diminution de leur valeur sélective, avec des conséquences dommageables sur leur aptitude compétitive. De la même manière, les EEE peuvent également affecter les espèces natives par perturbation des réseaux mutualistes pollinisateurs et symbiotiques (Stinson *et al.*, 2006; Schweiger *et al.*, 2010).

De nombreuses espèces exotiques envahissantes végétales sont, ou sont susceptibles d'être, supérieures compétitivement aux espèces natives par leur capacité à libérer des composés allélopathiques dans l'environnement (Del Fabbro & Prati, 2015) via une exsudation racinaire (Abgrall *et al.*, 2018) ou lors de la dégradation de leur matière organique sénescente aérienne comme racinaire (Inderjit *et al.*, 2011a). L'allélopathie est définie par la capacité d'un organisme à produire un, ou plusieurs, composés chimiques influençant la germination, la croissance, la survie ou la reproduction d'autres organismes (Inderjit *et al.*, 2011b; Rice, 2012). Ces composés forment un sous-ensemble des métabolites secondaires (composés organiques non impliqués dans la croissance, le développement ou la reproduction d'un organisme). Bien que les composés allélopathiques puissent avoir des effets positifs comme négatifs il est fréquemment considéré que, de par leur évolution distincte, les EEE apportent des composés contre lesquels les espèces natives ont peu, ou pas de défense (« armes nouvelles » ; Table 1-2). Ces effets peuvent instantanés ou persister dans le temps même en cas d'élimination de l'EEE (« héritage » ; Del Fabbro and Prati, 2015). Il y a une nécessité pour toute plante de trouver un compromis entre les bénéfices compétitifs (alloués par l'inhibition du développement des autres espèces environnantes) et l'investissement en ressources nécessaire à la synthèse de ces métabolites (Parepa & Bossdorf, 2016). L'efficience accrue d'utilisation des ressources de beaucoup d'EEE peut ici leur être bénéfique, en permettant une allocation plus importante de ressources au métabolisme secondaire, dans leur compétition avec les espèces natives (Funk & Vitousek, 2007).

### *3.2. Sur le fonctionnement des écosystèmes*

Les modifications susceptibles d'être induites par les invasions biologiques végétales sont nombreuses et dépendantes à la fois des espèces invasives elle-même, de la nature de l'écosystème, du climat, de la durée de l'invasion et d'autres facteurs encore. Les généralisations appliquées aux espèces exotiques envahissantes sont donc difficiles. Quelques exemples d'effets potentiels peuvent en revanche être discutés. La partie 3 de l'introduction traite des effets potentiellement applicables aux modèles d'étude utilisés lors de ces travaux de thèse.

Les invasions biologiques sont susceptibles d'altérer la taille des stocks d'éléments à l'échelle des écosystèmes (Ehrenfeld, 2010). Les stocks de carbone et d'azote aériens et souterrains tendent ainsi à augmenter suite à une invasion végétale (Ehrenfeld, 2003; Liao *et al.*, 2008a; Fraterrigo *et al.*, 2011; Martin *et al.*, 2017) et semblent également augmenter dans le cas du phosphore (Ehrenfeld, 2010). Comme mentionné plus haut ces patrons diffèrent en fonction de la forme de vie de l'EEE et selon les écosystèmes envahis. Des cas inverses sont toutefois fréquemment observés, notamment par certaines herbacées exotiques envahissantes (Bradley *et al.*, 2006). Ces différences, au moins pour le carbone, semblent plus liées aux différences de traits entre espèces natives et exotiques qu'aux valeurs absolues de ces traits chez les EEE (Vilà *et al.*, 2011; Castro-Diez *et al.*, 2014; Martin *et al.*, 2017). Certains groupes particuliers d'EEE végétales, comme les arbres fixateurs d'azote, ont un impact plus drastique encore sur la taille du stock d'azote (Rice *et al.*, 2004; Yelenik *et al.*, 2007; Ehrenfeld, 2010).

Les espèces exotiques envahissantes végétales altèrent fréquemment la quantité, qualité et phénologie de la litière produite à l'échelle de la communauté envahie (Standish *et al.*, 2004; Yelenik *et al.*, 2004; Ehrenfeld, 2010; Arthur *et al.*, 2012; Meisner *et al.*, 2012). Ceci implique un apport supplémentaire au sol, corroboré par l'augmentation fréquente des stocks mentionnée plus haut. La litière produite par les EEE tend également à se décomposer plus vite que celle des espèces natives (Ehrenfeld, 2010) notamment grâce une qualité chimique supérieure [ratios : C/N ou lignine/N réduits (Rice *et al.*, 2004; Standish *et al.*, 2004; Liao *et al.*, 2008a)]. L'augmentation de l'apport en litière tend également à augmenter les flux, notamment d'azote (Liao *et al.*, 2008a) avec ici encore des variations entre espèces (Ehrenfeld, 2010), entre sites pour une même espèce (Yelenik *et al.*, 2007) ou dans le temps (Yelenik & D'Antonio, 2013; Staska *et al.*, 2014). On observe aussi fréquemment des changements dans la disponibilité des nutriments (Standish *et al.*, 2004; Bohlen, 2006; Steidinger *et al.*, 2019).

L'altération des flux au sein d'un écosystème induite par les espèces invasives végétales peut aboutir à un changement de la répartition de ces stocks entre les compartiments endogés et épigés (Ehrenfeld, 2003; Liao *et al.*, 2008a). Une production primaire nette accrue est commune en cas d'envahissement végétal (Funk & Vitousek, 2007; Liao *et al.*, 2008a; Van Kleunen *et al.*, 2010b). Les EEE fixatrices d'azote peuvent modifier profondément les entrées d'azote dans l'écosystème (Vitousek & Walker, 1989). Des EEE sans symbioses rhizobiennes peuvent aussi avoir le même effet en favorisant ou inhibant l'activité des bactéries fixatrices d'azote vivant libres dans le sol (Ehrenfeld, 2010). Une production primaire implique, ou est causée par, une biomasse aérienne végétale plus importante dans les sites envahis par des espèces exotiques (Yelenik *et al.*, 2007; Ehrenfeld, 2010; Litt & Steidl, 2010; St.John *et al.*, 2012; Martin *et al.*, 2017). Ces modifications de la structure de l'habitat (Litt & Steidl, 2010) se répercutent sur la végétation (Van Couwenberghe *et al.*, 2011), la faune (Salmon &

Ponge, 2012; Costa *et al.*, 2013; Heiniger *et al.*, 2014) et le fonctionnement général des écosystèmes (Reich *et al.*, 2012). Dans certains cas les invasions biologiques végétales peuvent également affecter les flux de sortie des écosystèmes en modifiant, par exemple, la respiration du sol ou la dénitrification (Ehrenfeld, 2010).

La teneur en eau du sol peut être négativement affectée par la profondeur d'enracinement ainsi que la saisonnalité de l'absorption active de l'eau (Potts *et al.*, 2010). Ces traits pouvant varier à l'échelle de la communauté végétale avec l'envahissement les EEE peuvent ainsi entraîner une diminution de la disponibilité en eau (Ehrenfeld, 2003, 2010; Hejda *et al.*, 2009). Les modifications dans la structure des peuplement, habitats ou la quantité de biomasse épigée associées aux invasions biologiques végétales peuvent modifier les régimes de feu dans les écosystèmes y étant soumis (Bradley *et al.*, 2006; Brooks *et al.*, 2006). Des incendies plus fréquents, ou plus rares, peuvent ainsi avoir des répercussions drastiques supplémentaires sur les communautés végétales et le fonctionnement des écosystèmes (Reich *et al.*, 2012; Snyman, 2014).

### *3.3. Sur la faune*

Le remplacement des espèces natives par une espèce exotique devenant dominante altère la quantité et la qualité de la ressource trophique végétale vivante (Litt & Steidl, 2010; Renčo & Baležentiené, 2015; Viketoft & van der Putten, 2015) et morte (Van Kleunen *et al.*, 2010a) avec des répercussions sur l'ensemble de la communauté à la fois en terme d'abondance et de richesse spécifique (arthropodes épigés : Spafford *et al.*, 2013; Litt *et al.*, 2014 ; réseaux trophiques : McCary *et al.*, 2016; David *et al.*, 2017 ; les organismes de la litière et de la rhizosphère : Zhang *et al.*, 2018).

Ces effets ont tendance à différer entre types de milieux, Litt *et al.* (2014) trouvant dans une revue de synthèse un effet positif des EEE sur l'abondance et la richesse en arthropodes épigés en milieux fermées (c.-à-d. milieux forestiers, arborés ou arbustifs) et un effet négatif en milieux plus ouverts. Inversement, une méta-analyse récente sur la faune épigée montre une réponse plus négative en milieux forestiers et humides qu'en prairie (McCary *et al.*, 2016). La croissance rapide et massive de beaucoup d'EEE végétales et la couverture accrue de leur canopée (Grotkopp & Rejmánek, 2007; Hejda *et al.*, 2009) pourrait ici expliquer les différences entre milieux en modifiant plus profondément la structure de l'habitat et la ressource trophique qu'en milieux ouvert. Des changements dans la structure de l'habitat sont susceptibles d'impliquer des changements dans le régime hydrique.

Les impacts sur les invertébré épigés semblent également varier fortement en fonction du niveau trophique et de du type de réseau (McCary *et al.*, 2016). McCary *et al.* (2016) ont ainsi trouvé par méta-analyse une réponse plus forte, et négative, sur les consommateurs primaires (c.-à-d.

herbivores et détritivores) que des consommateurs secondaires (c.-à-d. prédateurs et microbivores). Qui plus est, cette réponse s'est avérée plus forte au sein des réseaux trophiques « vert » (basés sur l'herbivorie) qu'au sein des réseaux trophiques « bruns » (basés sur la détritivorie). Au sein des communautés aériennes, les herbivores tendent à une spécialisation plus importante envers leur ressource trophique (Litt *et al.*, 2014) que les détritivores, plus généralistes, ou les prédateurs (Scheu & Setälä, 2002). Zhang *et al.* (2019) ont également observé un effet positif des EEE végétales sur l'abondance des détritivores au travers de l'apport en litière, tout en démontrant un effet négatif sur les herbivores racinaires au sein de la rhizosphère. Cette même analyse démontre également un effet positif ou neutre de la litière d'EEE, et un effet négatif ou neutre de la rhizosphère, sur les consommateurs secondaires que sont les macrobiotes et les prédateurs. De nombreuses études de cas confirment qu'au sein des communautés animales, les herbivores sont généralement les plus impactés (Procheş *et al.*, 2008; Hartley *et al.*, 2010; Spafford *et al.*, 2013; Litt *et al.*, 2014)

L'effet des invasions biologiques sur la faune du sol fait l'objet d'une méta-analyse intitulée « **Soil responses to invasive alien plants are determined by trophic groups and habitat structure : a global meta-analysis** » en Chapitre 1 (p. 36) de ce manuscrit.

Un article intitulé « **Shifts and linkages of functional diversity between above- and below-ground compartments along a flooding gradient** », est ajouté au manuscript en Appendice (p. 169). Ces travaux ont été préparés pour publication au cours de cette thèse d'après des travaux réalisés lors d'un stage de seconde année de master. Ils illustrent les relations entre communautés végétales et animales édaphiques dans un contexte fortement contraint par un stress permanent et des perturbations occasionnelles. Les perturbations étant fréquemment une cause ou une conséquence des invasions biologiques ces travaux, bien que ne traitant pas des invasions biologiques, peuvent être d'intérêt dans le contexte de cette thèse.

## 4. Les modèles d'étude

Deux plantes exotiques envahissantes, documentées dans la littérature comme transformatrices, ont servi de modèle dans le cadre de cette étude : le robinier faux-acacia et la renouée du Japon. Ces deux plantes figurent dans plusieurs les listes des pires espèces exotiques végétales à l'échelle mondiale de par leur caractère envahissant et transformateur (Lowe *et al.*, 2000; Richardson & Rejmánek, 2011; Cronk & Fuller, 2014).

### *4.1. Le robinier faux-acacia*

Le robinier faux-acacia (*Robinia pseudoacacia* L.) est un arbre à feuilles caduques, à bois dur et de taille moyenne (10-30 m) de la famille des Fabacées, originaire de la région des Appalaches dans l'est des Etats-Unis (Figure 8). Il s'agit d'une essence pionnière héliophile de l'étage collinéen à optimum mésophile (milieux mésoxérophiles à mésohygrophiles ; Rameau *et al.*, 1989). Les individus sont hermaphrodites, la floraison a lieu de mai à juillet, la fécondation est assurée par zoogamie et des gousses plates à l'automne et persistant tout l'hiver accrochées aux branches fonctionnant comme une banque, ou réserve, de graines (Masaka *et al.*, 2013; Giuliani *et al.*, 2015). Il est également fortement drageonnant, ce qui contribue à sa capacité importante de dispersion (Benesperi *et al.*, 2012; Cierjacks *et al.*, 2013).

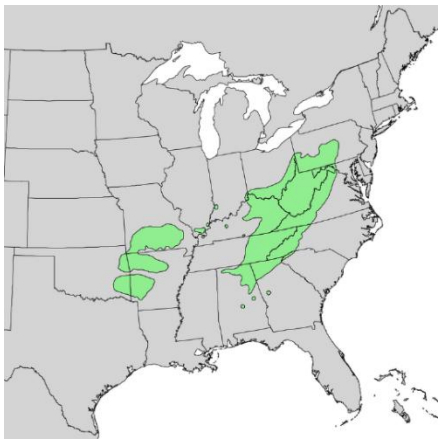


*Figure 8: Carte de l'aire de répartition naturelle du Robinier faux-acacia en Amérique du Nord. Carte dans le domaine publique issue de l'Atlas des arbres des Etats-Unis par Elbert J. Little Jr. (1971)*

Le robinier pseudoacacia est un des premiers arbre originaire d'Amérique du Nord introduit en Europe, au début du XVII$^{ème}$ siècle (Vítková *et al.*, 2017). Il s'agit d'une des espèces ligneuse les plus plantée à l'échelle mondiale (Keresztesi, 1988) notamment grâce à sa croissance rapide et son bois de haute qualité (Wei *et al.*, 2009). Il a également été planté en France, principalement dans la forêt privée de par la réticence des organismes publics de gestion forestière, il représentait en 2006 1% de la surface forestière (Figure 9 ; CRPFN, 2010).

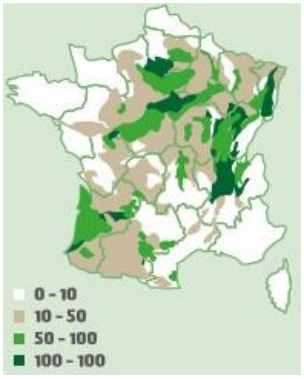



*Figure 9: Carte du volume sur pied en robinier en m³ par km² par région forestière en France métropolitaine. Source : Inventaire forestier national (IFN), 2001.*

Le robinier est classifié comme « hautement envahissant » dans plusieurs bases de données Européennes (EPPO, 2001; DAISIE, 2006a) et internationales (CABI, 2014) et est inclus dans plusieurs listes noires de pays Européens mais ne l'est pas dans les listes Européennes,

notamment à cause de pressions de certains pays membres ayant un intérêt économique fort pour cette espèce (Vítková *et al.*, 2017). Comme pour beaucoup d'espèces exotiques la transition entre naturalisation en envahissement a impliqué une longue phase de latence entre son introduction au XVII$^{ème}$ siècle et l'envahissement des XX$^{ème}$ et XXI$^{ème}$ siècles (Vítková *et al.*, 2017). Cet envahissement aurait été facilité par l'émergence des milieux urbains et industriels et le réchauffement relatif récent (naturel comme anthropique ; Sukopp and Wurzel, 2003). Qui plus est, le robinier investit une quantité importante de ressource dans la reproduction sexuée (Castro-Diez *et al.*, 2014) et asexuée (Rice *et al.*, 2004) facilitant ainsi son envahissement.

La distribution du robinier en Europe est contrainte par le climat, les propriétés du sol, la compétition interspécifique et l'existence de perturbations récurrentes (Cierjacks *et al.*, 2013; Li *et al.*, 2014; Vítková *et al.*, 2017). L'essence est peu tolérante à l'engorgement récurrent et de long-terme en eau, causant une anoxie racinaire, et à une compaction trop importante des sols. Le robinier préfère donc les sols aérés mais tolère des sols acides et basiques, riches ou pauvres en nutriments. Les conditions climatiques de l'aire de répartition native du robinier sont : -4 à 7 °C en moyenne en janvier, 18 à 27 °C en août avec des précipitations annuelles de 1020 à 1830 mm (Cierjacks *et al.*, 2013). Une étude par Li *et al.* (2014) a cherché à évaluer le potentiel global de distribution du robinier faux-acacia en fonction des conditions climatiques par modélisation reliant les données d'observations du robinier à 13 variables climatiques (Figure 10). Parmi ces variables cinq suffisent à expliquer plus de 80 % de la distribution spatiale du robinier : (i) le nombre de mois dont les températures moyennes sont inférieures à 5 ° C (27,92 % d'explication de la distribution) ; (ii) la température annuelle moyenne (22,03 %), (iii) le nombre de mois dont la température moyenne dépasse 5 °C (15,84 %), (iv) la température moyenne du mois le plus froid (8.96 %) et (iv) les précipitations annuelles moyennes (7,68 %). Le (i) correspond à une contrainte sur la maturation automnale des fruits et le (iii) une contrainte sur la foliaison et la floraison lors de la période estivale de croissance (Li *et al.*, 2014). L'optimum annuel moyen correspond quant à lui à une température de 5,8 à 14,5 °C et à des précipitations de 508-1867 mm. Si les températures diffèrent peu de celles rencontrées dans l'aire native il semble que le robinier soit plus tolérant à la sécheresse dans les zones qu'il envahit, accroissant ainsi son aire potentielle de distribution. Il semble aussi que les changements climatiques puissent accroitre la propension du Robinier à envahir les milieux naturels (passant de *e* à *f*, le dernier filtre environnemental, sur la Figure 3 ; Kleinbauer *et al.*, 2010) et le rendent plus compétitif dans de nombreux milieux de par sa large amplitude écologique (Li *et al.*, 2014). C'est également ce qui fait que le robinier a été suggéré comme essence de remplacement face aux conséquences des changements climatiques, avec des conséquences probables sur son potentiel d'envahissement (Duchiron & Schnitzler, 2009).

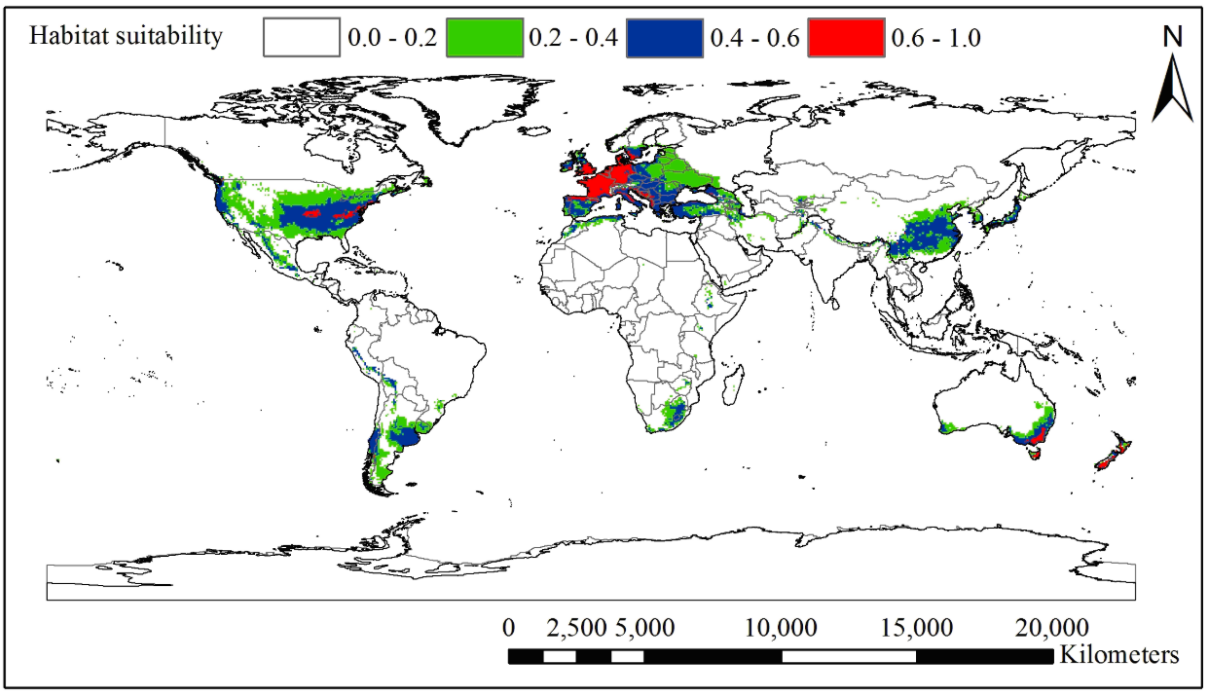



*Figure 10: Distribution potentielle globale du robinier faux-acacia prédite par le modèle MaxEnt basé sur les données climatiques stationnelles (Température : annuelle moyenne, moyenne du mois le plus chaud du mois le plus froid, écart annuel ; Précipitations : annuelles, du mois le plus sec, du mois le plus humide, saisonnalité ; évapotranspiration potentielle ; index d'humidité, de chaleur et de froid). Les couleurs désignent la capacité d'accueil potentielle relative de l'habitat pour le robinier de 0 (blanc) : inconvenant 1 (rouge) : optimal. Extrait de Li et al. (2014).*

L'une des caractéristiques principales du robinier, en tant que Fabacée, est qu'il possède des nodosités contenant des bactéries fixatrices d'azote atmosphérique (Franche *et al.*, 2009). Cette particularité permet l'acquisition indirecte de l'azote atmosphérique ($N_2$) pour le robinier en échange de glucides produits par photosynthèse et lui confère en partie sa capacité à croître dans des milieux pauvres et dégradés (Wei *et al.*, 2009). Cette fixation d'azote tend à causer une augmentation de la teneur en azote des sols où le robinier est présent (*e.g.* Rice *et al.*, 2004) mais cet effet dépend beaucoup des conditions initiales, notamment de la teneur initiale en azote, du milieu (Terwei *et al.*, 2016). Si l'azote n'est pas limitant il ne semble y avoir que des modification mineures dans le milieu. Le robinier est principalement mycorhizé par des endomycorhizes arbusculaires (AM) avec une rétroaction positive accrue par ces organismes dans l'aire native par rapport à l'aire d'invasions (Callaway *et al.*, 2011). Inversement les mycorhizes par des ectomycorhizes (EM) semblent proportionnellement plus rares que chez d'autres espèces (Taniguchi *et al.*, 2007a). Les AM tendent à augmenter l'aire racinaire spécifique et favoriser l'absorption de phosphore inorganique tandis que les EM tendent à favoriser l'absorption d'azote inorganique (Kubisch *et al.*, 2015). Dans la mesure où la symbiose rhizobienne fournit une source importante d'azote au robinier la symbiose ectomycorhizienne serait alors facultative. Les études globales montrent que les symbioses rhizobiennes sont communes dans les milieux chauds et secs mais relativement rares dans les forêts

mixtes tempérées (Steidinger *et al.*, 2019), où le robinier, quand il est présent, fait donc figure d'exception.

L'enrichissement en azote des sols est, quasiment systématiquement, la raison principale mentionnée dans la littérature pour l'inclusion du robinier faux-acacia dans la catégorie des espèces exotiques envahissantes transformatrices, ou « invasives » *sensu lato* (*e.g.* Cierjacks *et al.*, 2013; Vítková *et al.*, 2017). L'augmentation de la teneur en azote en présence du robinier (jusqu'à 75 $kg.ha^{-1}$ supplémentaire par an ; Boring and Swank, 1984) semble en effet faire consensus (Rice *et al.*, 2004; Landgraf *et al.*, 2005; Taniguchi *et al.*, 2007b; Rahmonov, 2009; Akamatsu *et al.*, 2011; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2015) même si elle n'est pas systématique (Von Holle *et al.*, 2006; Terwei *et al.*, 2016). Il s'agit ici de l'une augmentation de la teneur totale en azote des sols incluant à la fois l'azote minéral et organique (Figure 11).

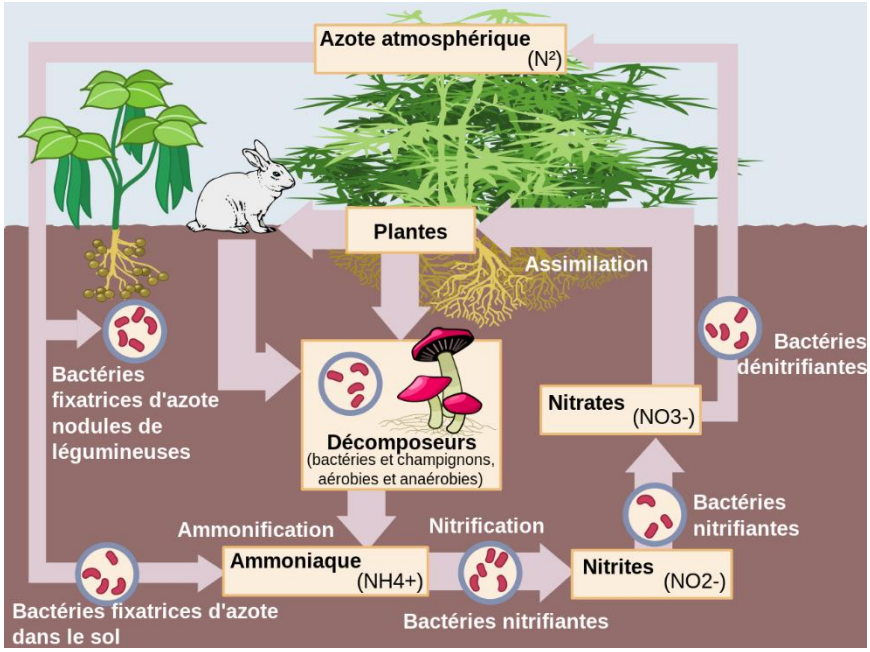



*Figure 11: Cycle de l'azote dans les sols et les différentes formes sous lesquelles il est présent. « Cycle de l'azote » par Johann Dréo (2006) sous licence CC BY-SA 2.5.*

Quelques auteurs ont différencié l'apport azoté du robinier en fonction de sa forme. L'azote organique est la forme dominante de l'azote dans les sols où il est contenu dans les molécules organiques (*e.g.* protéines, macromolécules polymérisées, etc). L'apport accru d'une litière riche en azote par le robinier semble effectivement affecter significativement ce pool d'azote (Landgraf *et al.*, 2005). La minéralisation de cet azote organique (c.-à-d. transformation vers une forme inorganique assimilable) dépend principalement de l'activité des microorganismes du sol. La décomposition de cette matière organique se fait par ammonification (Figure 11) transformant, en plusieurs étapes et

grâces aux bactéries ammonifiantes, l'azote contenu dans les molécules organique en ammoniaque ($NH_3$), qui est généralement retenue dans les sols sous forme ioniques, ou ammonium ($NH_4^+$). Les études ayant mesuré la teneur en ammonium dans les sols sous robinier n'ont généralement pas trouvé de différences par comparaison aux parcelles voisines dominées par des essences natives (Pereira *et al.*, 2011; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2016) malgré une possible augmentation automnale de l'ammonification (Pereira *et al.*, 2011). L'azote réduit ($NH_3$ ou $NH_4^+$) est ensuite oxydé en nitrite ($NO_2^-$), puis nitrate ($NO_3^-$), dans un processus appelé nitrification (Figure 11) réalisé par des bactéries et archées nitrifiantes. Le taux net de nitrification augmente drastiquement dans les sols où le robinier est présent (Rice *et al.*, 2004) avec, là encore, une variabilité saisonnière importante (Pereira *et al.*, 2011). Les nitrates sont généralement, dans les écosystèmes où la nitrification a lieu, la forme principale de l'azote pour son assimilation par les plantes. Dans la littérature, la teneur en nitrate dans les sols augmente quasiment systématiquement en présence du robinier (Rice *et al.*, 2004; Pereira *et al.*, 2011; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2016).

Cette augmentation de la teneur en nitrate, assimilable par les plantes, semble dans de nombreux cas favoriser la présence d'espèces végétales de sous-bois nitratophiles (Benesperi *et al.*, 2012; Cierjacks *et al.*, 2013; Staska *et al.*, 2014) et causer également la disparition de beaucoup d'espèces oligotrophes et acidotrophes typiques des peuplements forestiers (Benesperi *et al.*, 2012). Comme pour l'augmentation de la teneur en azote en elle-même, cet effet semble dépendant des conditions initiales du milieu (Terwei *et al.*, 2016). La présence du robinier faux-acacia semble alors être responsable d'une homogénéisation du milieu, ou au moins transformation, suffisante pour modifier la composition des communautés végétales de sous-bois. On observe ainsi fréquemment une diminution de la richesse spécifique et de la diversité des espèces végétales de sous-bois (Peloquin & Hiebert, 1999; Rice *et al.*, 2004; Benesperi *et al.*, 2012) même si cette diminution n'est pas systématique (Akatov *et al.*, 2012; Sitzia *et al.*, 2012; Masaka *et al.*, 2013; Von Holle *et al.*, 2013). Certains auteurs ont également observé une augmentation du nombre d'espèces exotiques, et de leur couverture, au sein des communautés végétales présentes sous robinier (Von Holle *et al.*, 2006, 2013) suggérant un possible effet cascade (Table 1 ; Simberloff and Holle, 1999).

La modification de la fertilité des sols n'est pas le seul facteur susceptible d'expliquer l'impact fréquent du robinier faux-acacia sur le sol et la végétation de sous-bois. Une diminution de la lumière disponible par une plus grande couverture semble également être une conséquence fréquente de la présence du robinier, surtout pendant les stades initiaux de la succession en milieu forestier (Sitzia *et al.*, 2012). Ce facteur est même considéré comme principal en cas d'envahissement de milieux ouverts (Kou *et al.*, 2016). Le robinier tend, notamment en tant qu'arbre pionnier de début de succession, à avoir des traits différents de ceux des essences natives environnantes en milieu forestier

(Grotkopp & Rejmánek, 2007) et cause une fermeture rapide de la canopée (<30 % en moins d'un an) dans une exclusion compétitive des autres essences de début de succession (Taniguchi *et al.*, 2007b), ce qui pourrait avoir des conséquences sur la diversité initiale des peuplements forestiers pouvant persister à plus long terme.

L'impact sur la faune du sol du remplacement d'essences natives par le robinier sont plus mal connues que ceux sur le fonctionnement du sol et sur la végétation native, malgré les interactions directes et indirectes entre les deux (Figure 5, Figure 7). Très peu de changement ont été observés dans la richesse spécifique ou la diversité (Brygadyrenko, 2015; Buchholz *et al.*, 2015; Della Rocca *et al.*, 2016) à l'exception d'une étude en Amérique du Nord par Degomez *et al.* (2001) comparant les communautés édaphique sous *R. pseudoacacia* et un congénère natif, *R. neomexicana*.

Les modifications des propriétés de la litière aérienne et souterraine, en terme de qualité, quantité et phénologie, liés aux différences de traits du robinier sont susceptibles d'affecter directement les consommateurs primaires des réseaux trophiques détritivores. La décomposition facilitée de la litière de robinier, notamment de février à mai quand la litière des espèces natives décompose peu (Lee *et al.*, 2011), est directement liée à l'activité des microorganismes décomposeurs et des macro-organismes fragmenteurs. L'apport important, notamment phosphaté, de litière au sol en période estivale par la chute des fleurs (Lee *et al.*, 2011) diffère de l'apport des essences natives environnantes (Medina-Villar *et al.*, 2015) et modifie donc la disponibilité temporelle de la resource trophique pour les fragmenteurs et décomposeurs. Brygadyrenko (2015) a ainsi observé une tendance à l'augmentation de l'abondance en saprophages au sein de la macrofaune du sol, notamment des isopodes. Della Rocca *et al.* (2016) n'ont, eux, pas observé d'effet des résidus ligneux de robinier sur les coléopères saproxyliques.

Aucune étude, à ma connaissance, n'a étudié l'effet sur les phytophages racinaires ou les herbivores de la litière. L'observation fréquente d'une diminution de la diversité des espèces de sous-bois laisse néanmoins supposer des répercussions potentielles sur ces organismes au vu de la spécialisation généralement importante des herbivores (Scheu & Setälä, 2002). Une étude, dans des forêts urbaines, laisse supposer un impact négatif sur l'abondance de certains taxons prédateurs (chilopoda et formicidae) mais pas tous (araneae et opiliones) qui pourraient être dû à une modification de la structure de l'habitat de ces organismes (c.-à-d. la litière, Buchholz *et al.* 2015).

### ***4.2. La renouée du Japon (Reynoutria japonica)***

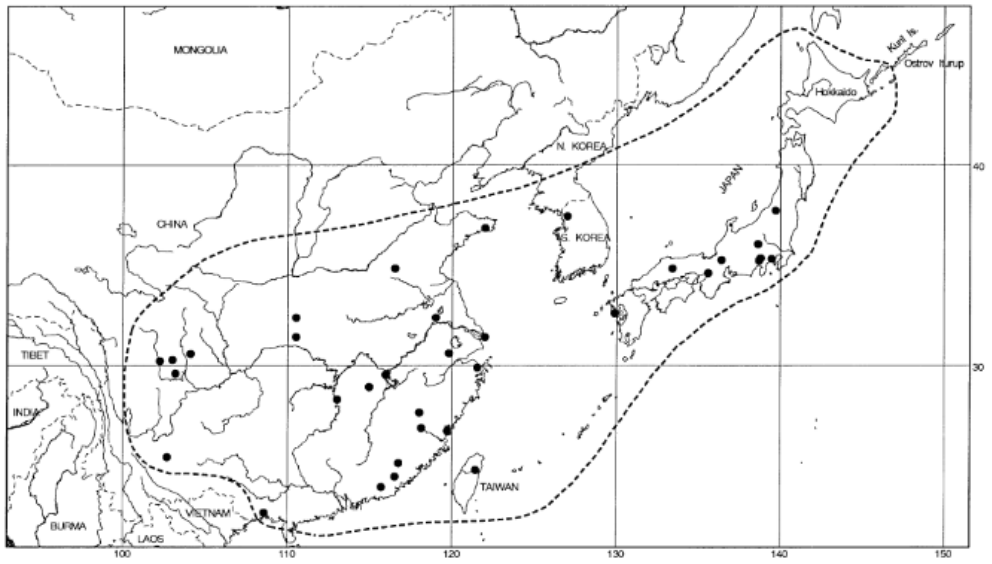



*Figure 12: Aire de distribution de la renouée du Japon en Asie du Sud-Est. Aire indiquée par le trait en pointillé, basée sur plusieurs sources [voir Beerling et al. (1995)]. Les points noirs indiquent les localités identifiées par nom, ou par les localités où des coordonnées de longitude et latitude ont été enregistrées. Extrait de Beerling et al. (1995) d'après Bailey (1989).*

La renouée du Japon [anciennement *Reynoutria japonica* Houtt, 1777, puis *Fallopia japonica* (Houtt.) Ronse Decr. 1988, puis à nouveau *R. japonica,* synonyme *Polygonum cuspidatum* Siebold 1846] est une plante herbacée pérenne de taille importante (2-4 m) appartenant à la famille des Polygonacées. Cette espèce est originaire d'Asie Orientale où elle est trouvée au Japon, en Corée ainsi qu'en Chine et à Taiwan (Figure 12; Beerling *et al.*, 2006). Une autre espèce du genre *Reynoutria*, la renouée de Sakhaline [anciennement *R. sachalinensis* (F.Schmidt) Nakai, puis *F. sachalinensis* (F.Schmidt) Ronse Decr., 1988, maintenant *R. sachalinensis*] partage une partie de son aire de répartition avec *R. japonica* (le nord de l'île principale de Honshū et l'île d'Hokkaidō ; Figure 12) et occupe également l'île de Sakhaline plus au nord où la renouée du japon n'est pas présente. Ces deux espèces ont été introduites en Europe (en 1825 pour *R. japonica* et 1869 pour *R. sachalinensis*) et en Amérique du Nord (XIX$^{ème}$ siècle) pour leur propriétés ornementales (Pyšek & Prach, 1993) et se sont depuis naturalisées. Ces deux espèces se sont hybridées en Europe donnant la renouée bohémienne (*R.* × *bohemica* (Chrtek & Chrtková) J.P.Bailey). Cette espèce a été fréquemment confondue avec *R. japonica* jusque dans les années 1980, rendant confuse une partie de l'historique d'envahissement de la renouée du Japon (Bailey & Wisskirchen, 2006).

La renouée du Japon est maintenant considérée parmi les 100 espèces exotiques envahissantes transformatrices les plus destructives au monde (Lowe *et al.*, 2000) et référencée dans toutes les bases de données comme fortement envahissante et transformatrice (« invasive » ; CABI, 2014; DAISIE, 2006b; EPPO, 2001; UICN, 2000). Comme beaucoup d'espèces exotiques envahissantes,

*R. japonica* et *R. sachalinensis* ont connu un délai important entre leur naturalisation (1848 et 1864, respectivement) et la première observation d'un envahissement caractérisé, dans les années 1930, soit près d'un siècle de latence (Bailey & Wisskirchen, 2006). La situation est assez similaire au Canada où le taux d'invasion a été maximal environ 70 ans après la naturalisation (Bourchier & Van Hezewijk, 2010). Les renouées du Japon introduites en Europe sont stériles, ne produisant pas de graines (Weston *et al.*, 2005). Cette particularité, qui pourrait être rédhibitoire pour une transition d'une espèce exotique naturalisée vers l'envahissement, ne l'est pas pour la renouée du Japon grâce à sa capacité importante de multiplication végétative et de régénération (Herpigny *et al.*, 2012). La *R. japonica* se propage donc majoritairement de manière clonale hors de son aire de répartition native, ou au moins dans sa zone d'envahissement Européenne, par le développement de rhizomes. Ces rhizomes peuvent s'étendre sur 15 à 20 m, et s'enfoncer jusqu'à 2 m de profondeur (Smith *et al.*, 2007).

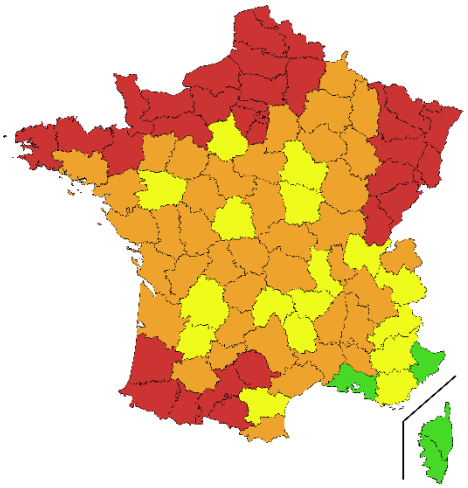


*Figure 13: Distribution de la renouée du Japon en France et par département en 2004. Rouge : plus de 100 localités, Orange : entre 11 et 100 localités ; Jaune : moins de 10 localités ; Vert : pas de localités connues. D'après Muller (2004).*

Dans son aire de répartition naturelle, on trouve *R. japonica* principalement dans les plaines inondables où elle occupe principalement les milieux ouverts au sein d'un cortège rudéral. On peut néanmoins la trouver également en altitude, jusqu'à 2500-2600 m, notamment en tant que pionnière de début de succession primaire de laves volcaniques où elle peut pousser à quelques centaines de mètre d'un cratère actif (SIVOA, 2004; Tucker Serniak, 2016). Ces milieux difficiles sont caractérisés par des rejets des cendres chaudes, de soufre, un pH faible, une faible fertilité du sol et une teneur forte en métaux lourds (SIVOA, 2004; Tucker Serniak, 2016). Il s'agit donc, même dans son aire de distribution native, d'une espèce extrêmement tolérante et résistante à large amplitude. En Europe, malgré le fait qu'elles puissent coloniser et se naturaliser jusqu'à 900 m on les retrouve majoritairement dans les plaines alluviales (Beerling & Dawah, 1993). Quelques individus ont néanmoins été retrouvés en Suisse jusqu'à 1400-1650 m (SIVOA, 2004). Il est probable que la renouée soit ici contrainte par son absence de reproduction sexuée et sa dépendance fréquente aux cours d'eau comme vecteur de dispersion de fragments de rhizomes, d'où son observation fréquente en milieux ripariens (Gerber *et al.*, 2008; Claeson *et al.*, 2014). Elle est également contrainte par des précipitations annuelles trop faibles (< 500 mm), une température moyenne annuelle trop froide (< 4 °C) et un nombre de jours de gel trop élevé (> 120 jours) (Beerling *et al.*, 1995; SIVOA, 2004).

Les propriétés impressionnantes de ses rhizomes ainsi que la capacité d'un simple fragment de rhizome de quelques grammes (régénération observée jusqu'à 0,7 g) à régénérer un individu complet en quelques dizaines de jours (Brock & Wade, 1992; Child, 1999) expliquent en grande partie la capacité de dispersion élevée de la renouée du Japon (De Waal, 2001). D'autres traits de la renouée du Japon lui sont particulièrement utiles en tant qu'EEE. L'élongation rapide des tiges (1 à 8 cm / jour ; Brock and Wade, 1992) et la capacité à développer rapidement une canopée dense lui confèrent une aptitude forte à la compétition pour l'accès à la lumière (Marigo & Pautou, 1998; Herpigny *et al.*, 2012) permettant l'exclusion compétitive d'espèces natives plus lentes dans leur développement. La quantité de biomasse produite par la renouée du Japon au cours de la saison de végétation atteint 1,6-4,5 $kg.m^{-2}$ pendant la saison de végétation, soit 1,8 à 5,7 fois la production de biomasse des communautés végétales natives environnantes (Dassonville *et al.*, 2008; Mincheva *et al.*, 2014). La taille plus importante de la renouée du Japon dans son aire d'envahissement (1 à 2 m supplémentaires) que dans son aire native (Holzner & Numata, 1982) laisse supposer une libération des ennemis naturels (Table 1-6) voire un mutualisme renforcé facilitant la croissance (Table 1-12). L'hypothèse de la libération des ennemis naturels semble également confirmée par la diminution drastique des dommages liés à l'herbivorie sur les parties aériennes de la plante (Maurel *et al.*, 2013) qu'on peut supposer similaire pour les parties souterraines, et qui a été confirmée pour certains pathogènes aériens et racinaires (Child & Wade, 2000). Les renouées ont également une efficience élevée dans l'utilisation de l'azote (Dommanget *et al.*, 2014) leur facilitant la colonisation de milieux pauvres en ressources nutritives où leur aptitude compétitive accrue les avantagerait contre les espèces natives oligotrophes et peu compétitives en terme de croissance. Ceci explique probablement la biomasse importante produite par la renouée du Japon. La densité même du réseau rhizomatique et racinaire est susceptible d'avoir des effets drastiques sur le compartiment sol, ceci couplé à d'autres caractéristiques telles que l'allélopathie.

Plusieurs espèces naturalisées du genre *Reynoutria* telles que *R. japonica*, *R. sachalinensis* et leur hybride *R.* × *bohemica* sont connues pour contenir et produire de nombreux métabolites secondaires (Murrell *et al.*, 2011). Certains de ces composés possèdent des propriétés allélopathiques et peuvent inhiber la germination ou la croissance d'autres espèces végétales (Gerber *et al.*, 2008; Aguilera *et al.*, 2010). Une concentration plus élevée en stilbènes, tel que le resveratrol, a été observée dans les tissus d'individus de *R. japonica* dans leur aire d'introduction et d'envahissement que dans leur aire de répartition native a été observée (Vastano *et al.*, 2000). Ceci suggère une sélection d'un trait favorable à l'envahissement de la renouée, ou l'évolution d'une aptitude compétitive supérieure (Table 1-7) ainsi que l'importance de la possession « d'armes novatrices » comme moyen d'exclusion des espèces natives facilitant la colonisation (Table 1-2 ; Callaway & Ridenour, 2004).

Le *Trans*-resveratrol (3,5,4'-trihydroxy-*trans*-stilbene) est un stilbénoïde, un type de polyphénol, produit par la renouée du japon (Vastano *et al.*, 2000) et d'autres végétaux (Pezet *et al.*, 1994; Vaher & Koel, 2003). Il s'agit d'un phytoalexine, des métabolites secondaires accumulés dans les tissus végétaux en réponse à une attaque d'un pathogène. Ces composés ont des propriétés antifongiques (Filip *et al.*, 2003) et antibactériennes (Chan, 2002) démontrées *ex situ*. Chez la renouée du japon 80% des *trans*-resveratrol sont contenus dans les rhizomes et les racines, lieu des interactions avec la microflore du sol mais également la micro- et mésofaune (Vaher & Koel, 2003). Un autre de ces polyphénols trouvés chez la renouée du Japon, flavonoïde, est la catéchine (Vaher & Koel, 2003; Vrchotova *et al.*, 2007).Plusieurs études ont démontré des répercussions de l'envahissement par la renouée du japon sur la microflore *in situ*, particulièrement les bactéries (Hedenec *et al.*, 2014). Malgré les propriétés antifongiques de ces composés en laboratoire, l'effet sur le terrain sur les champignons est mitigé par d'autres facteurs. Les propriétés récalcitrantes de la litière, produite en grande quantité, entraînent une décomposition lente favorisant les champignons par rapport aux bactéries (Tamura & Tharayil, 2014; Stefanowicz *et al.*, 2016). Ceci est notamment dû à une concentration élevée en tannins dans la litière favorisant là encore la voie fongique (Suseela *et al.*, 2016) en nécessitant la présence enzymes d'origine principalement fongique pour leur dégradation (Suseela *et al.*, 2016). A noter, cependant, qu'un impact négatif sur les mycorrhizes arbusculaires a été observé dans de nombreux cas, la renouée du Japon n'étant pas mycorrhizée (Stefanowicz *et al.*, 2016; Zubek *et al.*, 2016). Au-delà de l'impact allélopathique direct sur la flore native (Urgenson *et al.*, 2009; Aguilera *et al.*, 2010; Maurel *et al.*, 2010) il peut donc y avoir un impact négatif indirect via l'inhibition des partenaires fongiques de ces espèces natives.

Les conséquences de l'envahissement par la renouée du Japon sur la faune du sol et de la litière sont plus mal connues. Il y a une influence forte sur les macroarthropodes du sol, surtout négative sur les herbivores et positive sur les détritivores (Kappes *et al.*, 2007; Gerber *et al.*, 2008; Topp *et al.*, 2008). L'impact négatif sur les herbivores endogés s'applique aussi pour les macroinvertébrés herbivores épigés qui subissent une diminution de leur richesse spécifique. Celle-ci est corrélée à la diminution de la richesse spécifique en plantes natives et ce sans diminution générale de l'abondance en macroinvertébrés, mais un effet fort sur les espèces les plus spécialisées (Stoll *et al.*, 2012; Claeson *et al.*, 2014). Certains composés phénoliques, similaires à ceux produits par la renouée du Japon, ont un effet répulsif sur la mésofaune (Asplund *et al.*, 2015), voir même toxique dans certains cas (Isman & Duffey, 1982). Les modifications démontrées au sein des communautés de microorganismes et de la microfaune laissent également supposer des répercussions négatives indirectes sur les taxons fongivores ou nématophages comme les acariens oribates (Skubala & Mierny, 2009).

## 5. Objectifs et hypothèses

Cette thèse a pour objectif l'approfondissement des connaissances sur les conséquences des invasions biologiques végétales sur les écosystèmes et communautés envahies et plus particulièrement sur le compartiment sol. Afin de combler un manque de connaissances sur le sujet des et de mieux comprendre l'impact des invasions biologiques sur le fonctionnement des écosystèmes une attention particulière est donnée à la réponse fonctionnelle et taxonomique des communautés de la faune du sol. Deux modèles d'étude principaux sont considérés : le robinier faux-acacia (*Robinia pseudoacacia*), un arbre exotique naturalisé et fréquemment envahissant, et la renouée du Japon (*Reynoutria japonica*), une plante herbacée exotique extrêmement envahissante et transformatrice.

Ces problématiques ont été abordées à différentes échelles :

- Globale : méta-analyse globale de l'impact des espèces exotiques envahissantes sur la faune du sol (Chapitre 1, p. 37)
- Continentale : comparaison de l'impact du robinier dans plusieurs régions réparties en Europe de l'Ouest (Chapitre 2, p. 57)
- Régionale : étude approfondie à l'échelle de la Normandie de l'impact du robinier par comparaison à plusieurs essences natives (Chapitre 3, p. 79)
- Expérimentale : étude en laboratoire de l'effet des composés allélopathiques de la renouée du japon sur la biocénose du sol (Chapitre 4, p. 105)

### ***5.1. Les invasions biologiques et la faune du sol (Chapitre 1)***

Des méta-analyses récentes portant sur les arthropodes et macroinvertébrés épigés (Litt *et al.*, 2014; McCary *et al.*, 2016) ainsi que sur la biocénose du sol (Zhang *et al.*, 2018) attestent d'une réponse forte des communautés animales aux invasions biologiques végétales et justifient des travaux primaires, mais également de synthèse, sur le sujet. La première partie de ces travaux de thèse est donc dédiée à cette synthèse, sous forme de méta-analyse, et teste l'hypothèse générale suivante :

**H1** : *Les invasions biologiques, de par leur présence et leur effet sur les écosystèmes, ont un impact fort sur les communautés de la faune du sol.*

La susceptibilité différenciée de différents écosystèmes, habitats et communautés végétales aux invasions biologiques, et à leur impact, suggère une réponse elle-même différenciée des organismes du sol appartenant à des communautés occupant des habitats distincts et appuie l'intérêt de vérifier la validité de l'hypothèse suivante :

**H1.1** : *Les communautés de la faune du sol occupant des habitats distincts fonctionnent différemment, modérant la réponse aux invasions biologiques végétales.*

Nous avons pu voir précédemment la diversité existant au sein de la faune du sol, tant en terme morphologique que fonctionnel et trophique. Cette observation, combinée aux résultats obtenus précédemment par d'autres auteurs (*e.g.* Litt *et al.*, 2014; McCary *et al.*, 2016; Schirmel *et al.*, 2016) suggère des réponses différenciées en fonction du sous-ensemble considéré au sein des communautés de la faune du sol justifiant la sous-hypothèse suivante :

**H1.2** : *Cette réponse pouvant dépendre de la nature de l'interaction des organismes du sol avec l'envahisseur, les réponses diffèrent ainsi selon le groupe trophique considéré.*

### ***5.2. Le robinier faux-acacia : cas d'étude à large échelle sur un arbre exotique fixateur d'azote en milieu forestier (Chapitres 2 & 3)***

Le robinier faux-acacia présente des différences fonctionnelles marquées avec les essences natives dominant les milieux forestiers dans son aire ouest-Européenne d'introduction et d'envahissement. Ces différences, notamment liées à sa capacité symbiotique de fixation de l'azote et à des différences de phénologies et de traits foliaires, laissent supposer un impact fort, et fréquemment démontré, sur le fonctionnement des écosystèmes et les communautés végétales et de la faune du sol. La seconde partie de ces travaux de thèse consiste à tester l'hypothèse générale suivante sur le robinier :

**H2** : *Le robinier faux-acacia, altère le fonctionnement des écosystèmes forestiers et affecte les communautés végétales natives et la faune du sol.*

Le climat constitue le second filtre à l'établissement des espèces exotiques et à leur envahissement, après la distance spatiale. Le climat influence également fortement le fonctionnement des écosystèmes (Fierer *et al.*, 2009; Martin *et al.*, 2017; Steidinger *et al.*, 2019)s. Il parait donc raisonnable de considérer de probables différences dans l'impact des EEE en fonction des différences climatiques d'où la sous-hypothèse suivante :

**H2.1** : *L'impact du robinier varie le long d'un gradient latitudinal de par les différences de climat et d'essences natives dominantes.*

Les différences de traits fonctionnels et d'histoire de vie entre EEE végétales et espèces natives expliquent fréquemment à la fois leur caractère envahissant et ce qui peut les rendre transformatrices. En prenant en compte deux essences natives, toutes deux dominantes localement, dans l'étude de l'impact du robinier une compréhension plus approfondie du phénomène parait probable. La deuxième partie de l'étude sur le robinier faux-acacia constitue principalement en tester la sous-hypothèse suivante :

**H2.2** : *L'effet du robinier va différer selon l'essence native utilisée comme contrôle natif, notamment de par les différences fonctionnelles entre essences natives.*

### ***5.3. La renouée du japon : cas d'étude d'un mécanisme potentiel d'effet des invasions biologiques sur les réseaux trophiques du sol et son fonctionnement (Chapitre 4)***

La renouée du Japon modifie profondément les écosystèmes qu'elle envahit en modifiant la structure de l'habitat, en déplaçant les espèces natives et modifiant le cycle des nutriments. Il s'agit également d'une plante allélopathique dont les métabolites secondaires ont des effets bien connus sur la végétation native. Les répercussions sur les réseaux trophiques du sol sont, en revanche, méconnues mais probablement importantes au vu des modifications observées sur le terrain sur les communautés de microorganismes et de la microfaune. La dernière partie de ce travail de thèse (Chapitre 4) a pour objectif de tester la validité de l'hypothèse générale suivante :

**H3** : *Les métabolites secondaires allélopathiques de la renouée du Japon ont un impact sur les communautés de la biocénose du sol et le réseau trophique décomposeur.*

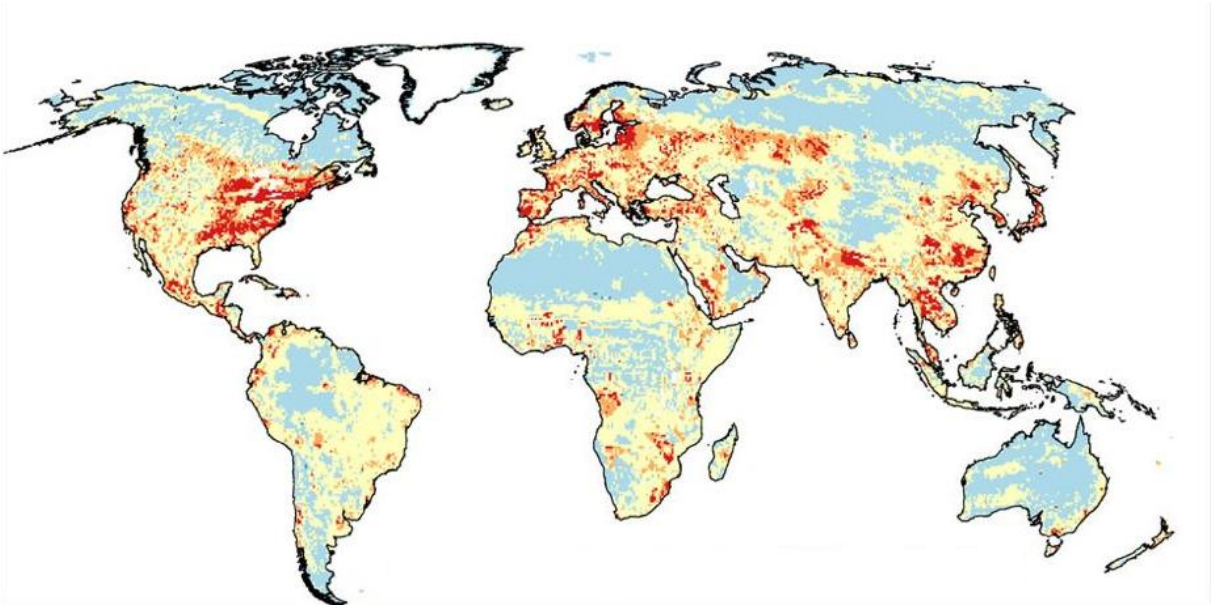
La littérature suggère et démontre un effet fort des métabolites secondaires de la renouée du Japon sur les microorganismes du sol. Ces conséquences modifient la disponibilité de la ressource trophique pour les organismes fongivores et bactérivores avec de possibles répercussions sur les niveaux supérieurs du réseau trophique. La sous-hypothèse suivante a été testée :

**H3.1** : *Les composés allélopathiques produits par les rhizomes de la renouée impactent négativement les microorganismes du sol. Cet impact se répercute négativement par cascade trophique aux niveaux supérieurs du réseau trophique.*

Les métabolites secondaires libérés dans la rhizosphère constituent également une source potentielle d'éléments nutritifs pour les microorganismes. Suivant leur nature, il est possible que cet apport mitige, ou compense, les effets négatifs allélopathiques de la renouée à la fois sur les microorganismes en eux-mêmes et les répercussions sur les maillons supérieurs du réseau trophique. Une seconde sous-hypothèse relative à ce questionnement a été testée au sein du chapitre 4.

**H3.2** : *La libération de ces composés dans la rhizosphère constitue également un apport nutritif, cet apport mitigeant ou compensant les effets négatifs allélopathiques sur la biocénose du sol.*

# Chapitre 1 – La réponse de la faune du sol aux espèces exotiques envahissantes végétales est modulée par les groupes trophiques et la structure de l'habitat : une méta-analyse globale.



**Risques globaux d'invasions au 21ème siècle**

Early *et al.* (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications, 7*. doi: 10.1038/ncomms12485)

# Soil fauna responses to invasive alien plants are determined by trophic groups and habitat structure: a global meta-analysis

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## Abstract

Despite increasing frequency of invasions by alien plant species with widespread ecological and economic consequences, it remains unclear how belowground compartments of ecosystems are impacted. In order to synthetize current knowledge and provide future directions for research we performed a meta-analysis assessing the impact of invasive alien plant species on soil fauna abundance. Compared to previous synthesis on this topic, we included together in our model the trophic group of each soil faunal taxa (from herbivores to predators) and habitat structure, namely open and closed habitats (i.e. grass and shrub dominated areas versus forested areas). In doing so, we highlighted that both moderators strongly interact to determine the response of soil fauna to the presence of invasive alien plants. Soil fauna abundance increases in the presence of invasive species only in closed habitats (+18.2%). This pattern of habitat-dependent response (positive effect in closed habitats) was only found for primary consumers (i.e. herbivores +29.1% and detritivores +66.7%) within both detritus-based and live root-based trophic pathways. Abundances of predators and microbivores did not respond to the presence of IAS irrespective of habitat structure. For several groups, the habitat structure (open or closed) significantly drove their responses to the presence of invasive alien species. In addition, we carefully considered potential sources of bias (e.g. geographic, taxonomic and functional) within the collected data in an attempt to highlight gaps in available knowledge on the subject. Our findings support the conclusions of previous studies on the subject by demonstrating (i) that soil fauna abundance is impacted by biological invasions, (ii) that initial habitat structure has a strong influence on the outcome and (iii) that responses within the soil fauna differ between trophic levels a stronger response of primary consumers.

*Keywords:* plant-soil interactions; global changes; biotic interactions; soil trophic groups; invasive alien species (IAS); soil communities

## 1. Introduction

Biological invasions are expected to increase over the next century threatening further negative impacts of biodiversity and ecosystem services (Vitousek *et al.* 1996, Mooney and Hobbs 2000, Reinhart *et al.* 2003, Van der Putten *et al.* 2007, Kumar 2010). Most research has concentrated on the effects of invasive alien plant species (henceforth referred to as IAS) on plants and aboveground animals (Bohlen 2006, Bellard *et al.* 2016). At present, it appears that IAS are likely to negatively affect native plant community richness and composition (Levine *et al.* 2003) with lesser effects on mammals, birds and reptiles (Crooks 2002, Schirmel *et al.* 2016). By comparison, relatively few studies have focused on the effects of IAS on soil fauna. Given the central role of soil fauna in ecosystem functioning, this represents a major knowledge gap in the effects of invasive plants.

Terrestrial ecosystems are composed of interacting aboveground and belowground compartments (Wardle *et al.* 2004) and biotic interactions regulate the structure and function of terrestrial systems as well as belowground fauna (e.g. Abgrall *et al.* 2017; Henneron *et al.* 2017). In the detrital food web plants indirectly influence fragmenter or decomposer organisms through the quantity and quality of litter (aerial or radical) entering the soil (McCary *et al.* 2016). In the root-based food web the characteristics of live roots directly modulate resource accessibility for root-associated organisms in antagonistic or mutualistic relationships. The detrital trophic pathway usually involves a relatively low level of specificity between plants and soil organisms while the reverse tends to be true for the root-based trophic pathway (Ali and Agrawal 2012).

Invasive species interact with both abiotic and biotic components of their environment when exploiting available resources. IAS frequently alter the quantity, quality and timing of litter production (Yelenik *et al.* 2004, Meisner *et al.* 2012) with repercussions on several processes such as litter decomposition, the accumulation soil organic matter and, in turn, nutrient release (Bohlen 2006, Zhang *et al.* 2019). In root-based trophic pathway, the drastic changes in plant communities that typically follow invasions can also result in altered quality and quantity of resources for root herbivores. Recently, Zhang *et al.* (2019) conducted a meta-analysis on IAS, the soil biota and nutrient cycling differentiating litter and rhizosphere effects. Based mostly on short-term manipulative experiments under controlled conditions they demonstrated that IAS litter had positive effect on several soil fauna trophic groups (detritivore and microbivore) with opposite rhizospheral effects on other groups (root herbivores andpredators). Their results suggest that IAS are prone to more negatively impact plant-based food webs than detrital food webs. However, as they underlined, the response of soil organisms under controlled conditions might strongly differ from field responses. Invasive plant species under

field conditions will establish complex relationships with belowground organisms and modify long-term processes with potentially different consequences.

The impact of invasive plants on plant-based and detrital foods webs might also be mediated by local plant communities' characteristics. McCary *et al.* (2016) demonstrated that the effects of IAS on grazing and detrital food webs clearly differed between different ecosystems. Invasive plants had the most pronounced effects on soil fauna trophic structure in wetlands and woodlands, with no detectable changes in grasslands. Ecosystem or habitat structure may strongly modulate the response of communities to IAS as illustrated with other disturbances and perturbations (e.g. Duhour *et al.* 2009; Slawska and Slawski 2017). Ecosystem functioning as well as plant and animal communities differ between open and closed habitats (e.g. Reich *et al.* 2012, Costa *et al.* 2013, Heiniger *et al.* 2014, Salmon *et al.* 2014). Open habitats are areas (e.g. grassland, tundras and some type of savannas) with low tree density while closed habitats (i.e forests) have a much higher tree density and canopy cover. These habitats differ in exposure to wind, rain and light with direct consequences to living organisms (water and light availability, desiccative stress through irradiance and temperature, etc). Differences in vegetation cover and stratification have repercussions on, with varying degree of generalizability, dissimilar net primary production, soil stratification, root biomass turnover, soil nutrient cycling, plant and animal community structure and other aspects of ecosystem functions (Bakker *et al.* 2006, Van Couwenberghe *et al.* 2011, Reich *et al.* 2012, Salmon *et al.* 2014). Differences in ecosystem dynamics and functioning can be expected to mediate the impact of invasive plant species on the soil fauna which are involved in numerous ecological processes and interactions with other organisms. To our knowledge, habitat structure (open vs closed) has never been explicitly considered in relation to the impact of biological invasion on soil compartments (but see McCary *et al.* (2016)).

In order to provide a comprehensive view of changes within belowground communities following invasion by exotic plants, we reviewed the scientific literature for data on the effects of invasive plants on the soil fauna using both a trophic group approach and by including habitat characteristics. We also provided a detailed analysis of potential biases in our data. We then tested, using meta-analytical techniques, the following hypotheses: (i) that organisms dependent on live root resources (i.e. herbivores) will be more negatively affected by invasion than organisms dependent on detritus (i.e. microbivores, detritivores) and (ii) that these effects are dependent on initial habitat structure, specifically that detritivores will be more readily impacted in open habitats.

## 2. Material & methods

### *2.1. Literature search*

We performed a literature search (from 1994 to 2017) using Web of Science Advanced Search feature with the following request: "TS=(invasive plant* OR invasive species OR "IAS" OR "invasive alien species") AND TS=(impact* OR effect* OR response*) AND TS=(soil fauna OR soil organism* OR soil invertebrate*)". Our literature search yielded a large number of results (2867). We selected 120 papers from their title (e.g. "invasive" in the medical sense of the word) before an in depth analysis of potentially appropriate papers from their abstracts and methodology. 47 were removed as they did not meet our criterion for inclusion in this review such as (i) not distinguishing between belowground and aboveground effects for taxa that inhabit all these strata (e.g. Collembola), (ii) studying non-native species exhibiting no invasion characteristics (i.e. not recorded in invasive species databases). 73 papers fit our criteria (see the list of these papers, and a synthesis of their results, Appendice B).

Several papers among the 73 tested the effect of IAS removal instead of invasion per se and were thus removed. In the end, out of these 73 papers (66 different IAS invading 20 countries) only 41 had sufficiently similar methodologies and included clearly defined 'control' (i.e. native vegetation) and 'invaded' groups to be included in a meta-analysis (Appendice B for details on which papers were retained for the meta-analysis). In addition to mean, variance (variance, standard deviation or standard error) and sample size within the two groups we extracted metadata on the identity of the invasive species (species and family), habitat structure (open or closed), geographical location (country/state and biogeographical region) and taxonomic/trophic group of the soil fauna. These papers considered the effect of 34 IAS from 17 families in 18 countries (see 'Bias evaluation' for details on potential taxonomic and biogeographic biases) on 11 taxonomic groups within the soil fauna. Soil fauna 'taxonomic groups' ranged from phylum (e.g. Nematoda) to order (e.g. Coleoptera) and, sometimes, family (e.g. Coleoptera: Carabidae). In total, combinations of individual IAS and taxonomic groups within the soil fauna enabled us to consider 159 independent cases. These results give general trends about the nature of interactions between invasive plants and soil fauna in relation to different habitat structure : "Open" areas include grasslands, tundras and other such herbaceous or shrub dominated habitats while "Closed" areas comprise forested areas. From each case we collected data on mean, standard deviation/variance and sample sizes of abundances of soil fauna in invaded and nearby uninvaded areas. We extracted meta-data regarding geographic location, habitat structure (open or closed), species name and family of the IAS considered taxonomic group within the soil fauna.

By considering trophic groups and their abundance we aim to minimize the problems inherent to considering only abundance data by providing more functional data on responses to IAs. Below we

differentiate between root-based and detritus-based components of soil food webs. Primary consumers in these trophic pathways are herbivores and detritivores, respectively. A detritivore is defined as an organism which feeds primarily on dead organic material, and is most commonly applied in terrestrial ecosystems to organisms that primarily consume plant detritus, with this definition does not preclude the possibility that acquisition of specific nutrients can be derived from live plant or microbial matter (Jumars *et al.*, 1984). Microbivores are secondary consumers within the detritus-based food web feeding primarily on decomposer microorganisms (i.e. primary consumers of plant litter). Predators, on the other-hand, are secondary or tertiary consumers able to ingest various types of organisms from both trophic pathways. This, combined with the low taxonomic resolution of available data and the overall lack of knowledge on belowground predators trophic preferences means that predators could not be assigned to a particular food web and are considered as belonging to both.

To assign feeding regime to the taxonomic groups, we used common trophic ecology papers dealing with soil food webs. In many instances, the authors of the primary studies detailed trophic groups in their analysis in which cases we assumed the trophic identification to be correct and directly used the data directly. Detrivores included earthworms (Lumbriculida), millipedes (Diplopoda), woodlice (Isopoda), Enchytreida (Haplotaxida) as well as some beetles (Coleoptera) when trophic group or detailed taxonomy was provided. Herbivores were mostly nematodes (when trophic group was given), Gasteropoda as well as some Coleoptera (both adults and larvae) when information was provided. Microbivores were nematodes (fungivorous and bacterivorous), some mites (Acari: Oribatida) and Collembola. Predators were spiders (Araneae), centipedes (Chilopoda), some mites (Acari: Gamasida), ground beetles (Coleoptera: Carabidae) as well as ants (Hymenoptera: Formicidae). Many groups within the soil fauna could not be assigned to a trophic group from taxonomy alone and were included in a group called “Other” (Appendice B). This approach allowed us afterward to study the impact of IAS on abundances of both taxonomical and trophic soil faunal groups.

### ***2.2. Statistical analysis***

We performed a meta-analysis on the collected data. The first step involved calculation of a standardized metric, the effect size, computed for each individual study or case enabling comparison between different studies. Effects size for individual studies were calculated using log response ratios (lnR) of abundances (A) in invaded and control areas in the form “log(A invaded / A control) (Doncaster & Spake, 2018). lnR are used when the outcome (i.e. effect size) is measured on a physical scale (i.e. is continuous) and has a natural zero point (i.e. “0” has meaning for the considered variable) (Hedges *et al.*, 1999). This is the case here as both abundance can be 0. lnR calculation use sample sizes, means and standard deviations from original studies, here for two ‘invaded’ (i.e. IAS present and dominant,

generally monospecifically) and 'control' treatments (i.e. native plant community still in place). lnR have been shown to be biased when quantifying the outcome of studies with small sample size (Lajeunesse, 2015). However, the author proposes revised and unbiased estimators for lnR which have since then been used in several ecological meta-analysis (e.g. Daryanto *et al.* 2016). Ratio of means (ROMs) were calculated using the 'metacont' function from package 'meta' (v4.8-4) (Schwarzer, 2007) using R Software (v3.4.2) which has methods for the unbiased lnR estimators. Each case is given a weight, the inverse variance, in order to minimize importance of small sample size cases in later statistical analyses.

We used random-effects models (i.e. unconditional inference about the general population) with maximum-likelihood estimator to evaluate moderators (i.e. variables) for inclusion. In such models, the considered studies are assumed to be a random sample, which is the case with our data (Hedges & Vevea, 1998). Mixed-effects models are random-effects model which include moderators (i.e. variables susceptible to predict effect sizes) that provide explanatory power for the variability in the data. We first wanted to test for an overall response of the soil fauna to plant invasions. We then tested for potential moderators of this hypothesized overall effect: trophic group and habitat structure as well as the interaction of both. All possible combinations of these three moderators, or lack thereof, were tested yielding 8 different models (see Table 2). We computed various estimators of model goodness-of-fit, model simplicity and overall model fit: AIC corrected for small sample sizes (AICc), log-likelihood (logLik) and the estimated amount of (residual) heterogeneity ($Tau^2$). AICc evaluates the trade-of between goodness-of-fit and model simplicity to avoid over- or underfitting. The log-likelihood quantifies how probable the observed data is with the considered model while $Tau^2$ provides an estimation of the proportion of residual heterogeneity after model fitting. We used the Bartlett correction of the likelihood ratio test (BcLR; Huizenga *et al.* 2011) and a pseudo $R^2$ statistic (Raudenbush, 2009) in order to evaluate and test the relative likelihood of each model compared to the 'Full' model with all moderators. A permutation test of moderators was also performed on each model (with the exception of the 'Null' model, with no moderators) in order to ascertain that the response to the moderators was not stochastic and therefore significant (Higgins & Thompson, 2004). Presented results are weighted means of effect sizes with their weighted standard errors of the mean. Model building was done using the 'rma' function in package 'metafor' (v2.0-0) (Viechtbauer, 2010) using R Software (v3.4.2) while model comparisons was done using the 'fitstats' function from the same package.

### ***2.3. Bias evaluation***

Practically all meta-analyses are prone to bias which can lead to incorrect inference. For instance, geographic bias is a common problem in meta-analysis as research efforts are often unevenly spread across countries. Most syntheses of existing data represent an opportunistic collection of studies that were designed for a wide variety of purposes (Gonzalez *et al.*, 2016). This is also the case for us: we collected any and all empirical data on differences in abundance between invaded and control areas. The main question then becomes whether this collected data is sufficiently representative of the current global distribution of invasive alien species, and thus their effect.

Using suggested methods from Martin *et al.* (2017) we used R package 'rvest' (Wickham, 2015) to collect (or 'scrape') data from the CABI Invasive Species Compendium (ISC; https://www.cabi.org/isc/) on the localization of documented invasive alien plant species. We then calculated the number of distinct documented IAS per biogeographic realm and the number of studies within our meta-analysis per biogeographic regions. Due to widely different values (34 vs 5863 IAS) we calculated relative number of species or studies per biogeographic realm (i.e. [0,1]). Following Gonzalez *et al.* (2016) we calculated the log ratio of the relative number of studies to the relative number of species per biogeographic realm. Positive values therefore indicate over-representation while negative values indicate under-representation.

While extracting data on geographic localization of IAS from the ISC we also extracted taxonomic tree information characterizing each species. We used taxonomic information to assess the representativeness of the considered taxa within our meta-analysis compared to worldwide IAS distribution. For that we used the log ratio of the relative number of cases per family within our meta-analysis to the relative number of IAS per family that contains IAS at a global level. 17 plant families were covered within our meta-analysis, out of a total of 250 families known, from the CABI database, to contain IAS (7%). These families, however, account for 53% of total number of recorded IAS.

We acquired trait data (plant vegetative height) from the TRY plant trait database (Kattge *et al.*, 2011) for all invasive species present in the ISC and for which data was available. Max height, in m, for each species was used instead of mean height. The frequent lack of information on growth stage height measurements makes the mean undesirable. We assigned each IAS in the CABI database to a height category on a log10 scale (categories based on Moles *et al.* 2009). As with biogeographic realm and plant family we compared relative distribution of species among height groups in the database data to the relative distribution in our meta-analytical data.

In order to assess the trend of publications over time within the literature we counted the number of publications per year from the earliest (excluding an article from 1977) to the latest and performed a linear regression on the data. Multiple soil fauna taxa were considered for meta-analysis with an uneven coverage among groups. We visually compared the coverage of the main soil fauna taxonomic groups considered for meta-analysis in order to reveal possible over- or underrepresentation of some taxa.

Publication bias occurs when the probability of publication depends on the statistical significance, magnitude or direction of the effect (Koricheva & Gurevitch, 2014). A review by Jennions and Moeller (2002) showed that publications bias may negatively affect the validity of the conclusions in 15-21% of meta-analysis in the field of ecology and evolution with 61% of the reviews not evaluating publication bias. Funnel plots are a simple graphical tool that can provide some indications on possible publication biases that is widely used in meta-analyses despite some important limitations (i.e. inaccuracies and unreliability in some cases; Lau, 2006). Other quantitative methods are frequently used to quantitatively assess for publication bias by testing for funnel plot asymmetry, such as Egger's regression test (Peters *et al.*, 2015). As a means to evaluate possible publication bias we constructed a funnel plot of sample size by effect size (observed outcome) to show possible magnitude-of-effect and direction-of-effect biases. Additionally, we plotted significance levels as given by the authors in the original papers to show possible significance-of-effect biases and displayed the results of an Egger's regression test.

## 3. Results

### *3.1. Biases*

There are discrepancies in representation of different biogeographic realms. Neartic and Australian realms are over-represented in the dataset compared to the documented distribution of IAS while Oceanian and Neotropical realms are under-represented (Figure 14a). Similarly there are some over-represented invasive plant families in our dataset such as Simaroubaceae (due to 2 studies on the tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle), with multiple studied soil fauna taxa) and, to a lesser extent, Balsaminaceae (*Impatiens glandulifera* Royle), Fagaceae (*Quercus robur* L.) and Zingiberaceae (*Hedychium gardnerianum* Sheppard ex Ker Gawl.) (Figure 14b). Similarly some height groups were overrepresented in the dataset such as shrubs and trees (1-10 m and 10-100 m groups) (Figure 14c). We also show a strong increase in the number of cases over time (Figure 14d). However this increase is probably correlated to the overall increase in the number of publication in ecology (ISI Web of Knowledge search for 'ecology') and the general trend of scientific publishing (Jinha, 2010). It appears likely that the trend will continue, at least for the immediate future.

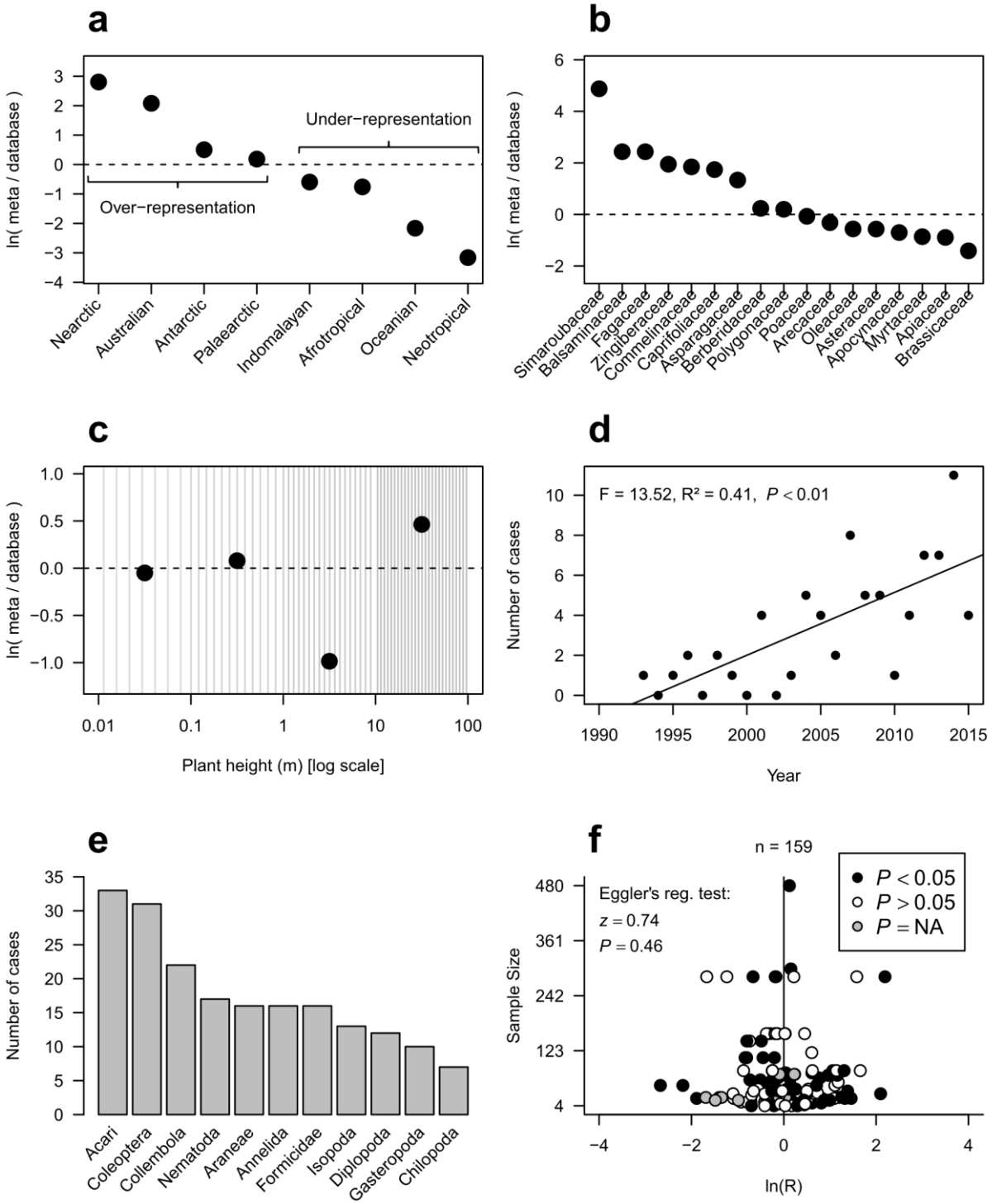



*Figure 14: Details on the collected dataset and exploration of potential biases. (a) Spatial biases in collected dataset. (b) IAS Taxonomic biases in collected dataset. (c) IAS Height biases in collected dataset. (d) Number of publications per year. (e) Number of cases per soil fauna taxa. (f) Funnel plot of the relationship between sample size, effect size and level of significance. For a-c, the y-axis shows the natural log of the odds ratio (lnOR) of data in meta-analysis and CABI database. Any lnOR y > 0 indicates that the category on the x-axis is represented ey % more in the meta-analysis than in the database. Any lnOR y < 0 indicates that the category on the x-axis is represented e-y % less in the meta-analysis than in the database. For d, a linear regression displayed to show trend over time. For f, results are from a mixed-effect meta-regression model without moderators. Level of significance are from the original papers. 'p = NA' indicate no statistical testing in the original paper.*

All the studies screened for this meta-analysis encompass only a small portion of the soil fauna and with varying exhaustiveness (Figure 14e). The data presented in Figure 1e shows a bias toward several groups, such as the mesofauna (here, Acari and Collembola), the microfauna (here, Nematoda) and representatives of the macrofauna such as Coleoptera. The latter being a cosmopolitan order featuring the highest number of species among insects and therefore frequently studied. These overrepresented groups are predominantly microbivores while specialized predators (such as Chilopoda or Araneae) and detritivores (such as Isopoda) are comparatively underrepresented.

We also checked for publication bias using the funnel plot method and Egller's regression test (Figure 14f). While not perfectly "funnel-shaped" the plot shows that studies with low-precision (i.e. low sample size) tend to show greater variability around the average than high-precision studies, which is the expected pattern. In addition there does not appear to be many gaps in the data that could suggest the existence of unpublished missing data. Finally we used a quantitative approach to test for asymmetry within meta-analysis results for which the null hypothesis was rejected (Figure 14f indicating symmetry within the data and thus, as per the test hypotheses, a lack of quantitative bias.

### ***3.2. Model comparisons***

BcLR test result showed that the observed data was significantly more probable under the 'Full' model ($z = \beta_0 + \beta_1 \cdot x + \beta_2 \cdot y + \beta_3 \cdot xy$) than under the reduced models tested (Table 2). The only exception was for the 'Habitat' model ($z = \beta_0 + \beta_1 \cdot x$) which fitted the data as well as the 'Full' model (BcLR = 13.52, $P > 0.05$). The permutation test of moderators (QM) results shows that in both the 'Full' (QM = 21.15, $P < 0.05$) and 'Habitat' (QM = 6.32, $P < 0.05$) models, the moderators effect on the response (*i.e.* effect sizes) is not due to chance and is therefore significant (Higgins & Thompson, 2004). These results show that the 'Full' and 'Habitat' models provide the best fits for the considered data (i.e. highest likelihood of the observed data) with the 'Full' model having the highest likelihood (logLik -164.25 compared to -171.01). Model selection though information criterions (*i.e.* AICc) shows that the 'Habitat' model offers the best compromise between goodness-of-fit and model simplicity (i.e. lowest values; Table 2). However, model selection tools tend to assign a high weight to model simplicity (i.e. number of estimated parameters) which is pertinent when constructing predictive models that would suffer from over-fitting but less so when constructing diagnostic models (Coelho & Alexandre, Diniz-Filho JoséRangel, 2018). In addition the table below shows that the 'Full' model improves the fit over both 'Habitat + Interaction' ($z = \beta_0 + \beta_1 \cdot x + \beta_3 \cdot xy$) and 'Trophic + Habitat' ($z = \beta_0 + \beta_2 \cdot y + \beta_3 \cdot xy$) models showing that both trophic level ($\beta_2$) and interactions ($\beta_3$) are of importance in explaining the observed data if only when included together with habitat ($\beta_1$). This model is also in accordance with previous work on

the subject showing differential responses of the soil fauna to invasive plant species depending on both habitat structure and trophic pathway (McCary *et al.*, 2016; Zhang *et al.*, 2018).

*Table 2: Model comparison test results without or with moderators. Moderators are 'Habitat' for open vs closed habitats and 'Trophic' for the trophic group of the soil fauna in invaded area and 'Interact.' for the interaction of both factors.*

| *Model* | *Equation* | *Df* | *AICc* | *logLik* | *QM* | *Tau²* | *BcLR* | *$R^2$ loss* |
|---|---|---|---|---|---|---|---|---|
| Full | $z = \beta_0 + \beta_1 \cdot x + \beta_2 \cdot y + \beta_3 \cdot xy$ | 11 | 352.34 | -164.25 | 21.15 * | 0.371 | / | / |
| Trophic + Interac. | $z = \beta_0 + \beta_2 \cdot y + \beta_3 \cdot xy$ | 10 | 359.22 | -168.85 | 10.88 n.s | 0.401 | 9.20 ** | 7.57% |
| Habitat + Interac. | $z = \beta_0 + \beta_1 \cdot x + \beta_3 \cdot xy$ | 7 | 353.45 | -169.34 | 9.72 n.s | 0.406 | 10.19 * | 8.80% |
| Interac. | $z = \beta_0 + \beta_3 \cdot xy$ | 6 | 354.87 | -171.15 | 5.93 n.s | 0.417 | 13.80 * | 11.24% |
| Trophic + Habitat | $z = \beta_0 + \beta_1 \cdot x + \beta_2 \cdot y$ | 7 | 352.95 | -169.10 | 10.46 n.s | 0.401 | 9.70 * | 7.29% |
| Trophic | $z = \beta_0 + \beta_2 \cdot y$ | 6 | 356.27 | -171.85 | 4.61 n.s | 0.419 | 15.21 ** | 11.64% |
| Habitat | $z = \beta_0 + \beta_1 \cdot x$ | 3 | 350.17 | -171.01 | 6.32 * | 0.414 | 13.52 n.s | 10.50% |
| Null | $z = \beta_0$ | 2 | 351.70 | -174.06 | / | 0.437 | 19.63 * | 15.12% |

'β0' = Intercept; 'β1' = Habitat moderator coefficient; 'β2' = Trophic level moderator coefficient; 'β3' = Interaction between habitat and trophic level moderator coefficient; 'Df' = Degrees of freedom; 'AIC' = Akaike Information Criterion; 'BIC' = Bayesian (Schwarz) Information Criterion; 'AICc' = AIC with correction for small sample size; 'logLik' = Log-likelihood of the model at the estimated coefficients; 'QE' = Test statistic for a test of (residual) heterogeneity; 'QM' = Test statistic for a permutation test of coefficients; 'Tau²' = Estimated amount of (residual) heterogeneity; 'BcLR' = Bartlett corrected likelihood ratio test between the full model and the corresponding reduced model; 'R²' = Amount of (residual) heterogeneity in the reduced model that is accounted for in the full model; 'n.s' = non-significant; '*' = P < 0.05; '**' = P < 0.01; '***' = P < 0.001

### ***3.3. Meta-analysis***

Herbivores belonging to the root-based trophic pathway were not influenced by the presence of IAS except in closed habitats where abundance was significantly higher after invasion (+29.1 ± 8.6%; Figure 14). The same pattern was observed for the abundance of detritivores belonging to the detritus-based trophic pathway (+66.7 ± 24.8% in closed habitats), with also a significantly different response between open and closed habitats ($W$ = 19, $p$ < 0.05; Table 3). Microbivores, also belonging to the detrital trophic pathway, did not show any significant changes in their abundances after invasion in closed, open habitats, or in both habitats combined.

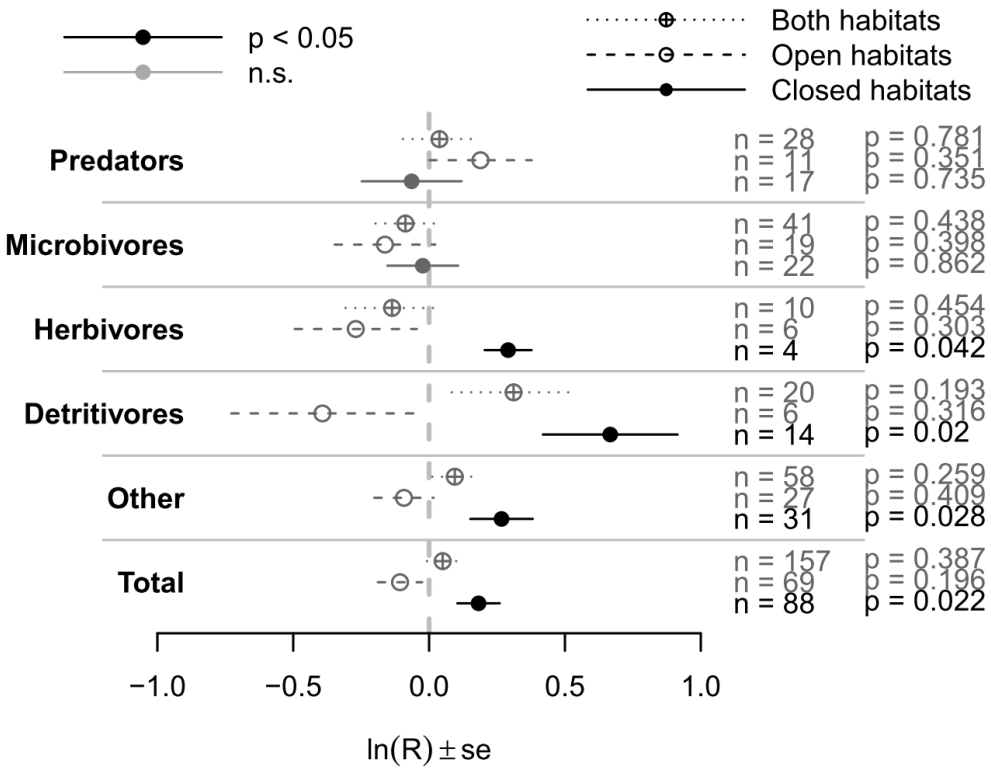



*Figure 15: Responses of the soil fauna to biological invasions according to trophic groups and openness of invaded habitat. Displayed are weighted means and standard errors of log-response ratios (ln(R)) for each considered category. P values are from weighted t*

While abundance of predators belonging to both trophic pathways also did not show any significant pattern, the other trophically unclassified groups and the total soil fauna, had a pattern similar to the detritivores and the herbivores, that is to say a higher abundance in closed habitats subject to invasion (+26.6 ± 11.5 % and +18.2 ± 7.8 % for unclassified and total groups, respectively). Furthermore, when considering all fauna data (total), then the response observed in open habitats significantly differed from the response observed in closed habitats (W = 2423, $p < 0.05$; Table 3).

*Table 3: Differences between open and closed habitats for each considered trophic group. Values are mean and standard error, statistics are for a two-sample Wilcoxon signed-rank test.*

| *Group* | *Habitat* | | *Sample size* | | *Wilcoxon test* | |
|---|---|---|---|---|---|---|
| | *Open* | *Closed* | *Open* | *Closed* | *W* | *p-value* |
| Detritivores | -0.392 (0.335) | 0.667 (0.248) | 6 | 14 | 19 | **0.042** |
| Herbivores | -0.270 (0.225) | 0.291 (0.086) | 6 | 4 | 5 | 0.171 |
| Microbivores | -0.162 (0.185) | -0.023 (0.130) | 19 | 22 | 186 | 0.560 |
| Predators | 0.189 (0.189) | -0.064 (0.184) | 11 | 17 | 120 | 0.226 |
| Other | -0.092 (0.109) | 0.267 (0.115) | 27 | 31 | 304 | 0.075 |
| Total | -0.107 (0.082) | 0.182 (0.078) | 69 | 88 | 2423 | **0.030** |

## 4. Discussion

Model comparisons showed that habitat structure explains a higher proportion of heterogeneity within the dataset than trophic group alone (Table 2). The importance of habitat characteristics or ecosystem type in invasion ecology was also highlighted by other authors such as McCary *et al.* (2016) and Liebhold *et al.* (2017). Overall, soil fauna abundance did not significantly change after plant invasion. This result contrasts with the hypothesis of a negative impact on the soil fauna (e.g. Maceda-Veiga *et al.* 2016; Morriën *et al.* 2012; Tanner *et al.* 2013) but it supports the findings of recent meta-analyses (McCary *et al.*, 2016; Zhang *et al.*, 2018). Impacts of IAS are as diverse as impacted organisms and, depending on considered variable, not necessarily negative (David *et al.*, 2017). We showed that prediction of IAS effects on soil fauna strongly benefits from including the trophic groups of impacted organisms as well as the habitat structure of the invaded ecosystems. Indeed, soil fauna abundance across all trophic groups increased following invasion in closed habitats (+18.2%) yet, as shown in Figure 15, this is not the case for predators and microbivores. This response is significantly different from the one observed in open habitats (Table 3). Habitat structure plays a fundamental role in the response of the whole soil fauna following invasion, as previously suggested (McCary *et al.*, 2016).

### *4.1. Root-based trophic pathway*

For belowground herbivores, our meta-analysis did not reveal any general response to IAS without taking into account the habitat structure (Figure 15). A negative effect of IAS on herbivore abundance had previously been observed by Zhang *et al.* (2019). Root herbivores are primary consumers and have direct relationships with IAS through, in our paradigm, delivery of trophic resources. There is evidence for a high level of specificity between aboveground organisms involved in direct relationships resulting from a shared evolutionary history (Litt *et al.*, 2014). Over 90% of aboveground insect herbivores, for example, feed only on plants belonging to a single genus or family (Ali & Agrawal, 2012). Accordingly, McCary *et al.* 2016 found that the abundance of aboveground herbivores declined in invaded areas dominated by one plant species, limiting resource choice for herbivores. In contrast, most of the root herbivores are rather generalists (Wallinger *et al.*, 2014). Thus, plant invasive status, belowground, may not play as important a role in driving abundances of herbivores as long as there are roots available for consumption.

We found that the abundances of belowground herbivores increased in closed habitats (+29.1 ± 8.6%). This is surprising as IAS are frequently rather unpalatable (Ernst & Cappuccino, 2005) and generally have reduced herbivore-damage compared to native species or themselves in their native range, at least aboveground (Keane & Crawley, 2002; Procheş *et al.*, 2008; Hartley *et al.*, 2010; Maurel

*et al.*, 2013; Litt *et al.*, 2014). But McCary *et al.* (2016) also found contrasting results for primary consumers aboveground within the herbivory-based pathway depending on ecosystem type. They found negative responses of above ground herbivorous primary consumers within closed habitats (i.e. forests), while our analyses showed the opposite for belowground herbivores, highlighting the difference in structure and functioning of above and belowground compartments.

### *4.2. Detritus-based trophic pathway*

Detritivore abundance showed no response across habitats yet were differentiated when considering closed vs open habitats (Table 3). We noticed an increase of their abundances (+66.7 ± 24.8%) in closed habitats, while in invaded open habitats their abundances tend to decline (-26.9 ± 22.5%). Detritivores have indirect, yet strong, relationships with IAS and native plants as they rely on dead organic matter as their food source (Sauvadet *et al.*, 2017). IAS, on average, produce more readily decomposable leaf litter than similar native species (Van Kleunen *et al.*, 2010b). In our case, these changes in litter properties following invasion may explain the contrasting responses of detritivores as litter produced by plants of open and closed habitats can differ in their quality (Bakker *et al.*, 2006). The ratio of lignin to nitrogen in tree leaf litter is also higher than the same ratio within graminoid or forb litter which can lead to faster litter decomposition in open habitats (Reich *et al.*, 2012). Invasive species may drastically change litter quality and the quantity deposited on the ground modifying the food resources and habitat structure for detritivores. The findings of Zhang *et al.* (2019) showed an increase of microbial activity (respiration) and of N mineralization when adding litter of invasive species. From our results, we can hypothesize that litter quality is enhanced in closed habitats following invasion favoring increased abundance of detritivores.

Microbivores (secondary consumers within the detrital trophic pathway) showed no response to IAS despite large sample sizes, particularly Collembola and Acari (Figure 14e; Figure 15). Microbivores are thought to be bottom-up controlled by either fungal or bacterial food sources (Polis & Strong, 1996). Zhang *et al.* (2018) in their recent meta-analyses found a lack of effect of IAS litter input on soil microbial, and fungal, biomass despite increased activity. Therefore, the lack of response of the soil microbivores is rather consistent with these previous findings.

### *4.3. Predators*

Soil predators are thought to be mainly generalists (Scheu & Setälä, 2002) and therefore they play a regulatory role on organisms of lower trophic levels belonging to both root-based and detritus-based pathways. Predators showed the same pattern as microbivores to the IAS presence (Figure 15), namely a lack of response irrespective of habitat structure.

Predators, in our context, are secondary or tertiary consumers of other organisms within the soil fauna. McCary et al (2016) also found no generalizable response of secondary consumers but Zhang *et al.* (2019) observed a negative response of predators to IAS in controlled experiments through a rhizosphere effect but not a litter effect. Diminishing abundances of organisms at lower trophic levels may lower the energy available to higher trophic groups, and by a bottom-up process to which they are sensitive, negatively impact soil predators (Tallamy, 2004; Mgobozi *et al.*, 2008). Indeed, decreased prey availability has frequently been considered the dominant factor explaining decreased predator abundance (i.e. bottom-up control) following invasions by exotic plants (Lindsay & French, 2006; Gerber *et al.*, 2008; Wolkovich *et al.*, 2009; Tanner *et al.*, 2013; Motard *et al.*, 2015). However, we could not support these findings even with a high number of cases (n = 28). Conversely, changes in habitat structure are often considered as responsible for increases in predator abundances following biological invasions (e.g. Gerber *et al.* 2008; Schirmel *et al.* 2011). Here again our results based on 11 and 17 cases (in open and close habitats, respectively) do not allow us to generalize this statement as the response of predators did not change in relation to habitat structure.

### *4.4. Caveats, biases & synthesis*

The model with the overall best fit for the empirical data was the full model taking into account both moderators (habitat structure and trophic group) as well as their interaction (Table 2). These moderators only account for a small fraction (15%) of the observed variability in the data which is common in ecological studies particularly at large scales. The main probable sources of variability within the dataset are the vastly different geographical contexts among considered studies as well as the number of different species (34 IAS in 41 studies). The first is partially alleviated by the paired nature of individual studies. The second, however, is more problematic as the impact of an individual IAS is more likely to be dependent on the traits that make them invasive rather than their identity. Plant functional traits have been shown to provide far better predictions of soil fauna community structure than plant identity itself (e.g. Fournier *et al.* 2012, Frenette-Dussault *et al.* 2013, Abgrall *et al.* 2017). In our case, it seems likely that including IAS functional traits such as litter and leaf quality and quantity, growth form or allelopathy would have provided a more mechanistic explanation to our results yet this would require traits to be measured by the authors of each study. Indeed, databases have been shown to provide frequently inaccurate trait information at the community level despite being useful at larger scales (Bekker *et al.*, 2013).

Despite these caveats, we found differences in direction, and intensity, of response for several trophic groups based on habitat structure, supporting our initial hypotheses. Specifically, half of the trophic groups responded significantly to the ingression of invasive species in closed habitats with

increased abundances. Litter quality is often more influential to the composition of soil fauna assemblages than root inputs when the fungal energy channel is dominant, such as in closed habitats, because the system is bottom-up (i.e. primary production) regulated (St. John *et al.*, 2006; Henneron *et al.*, 2017). This will strongly depend on biomass production of IAS and we showed in Figure 14 a positive bias towards IAS with heights of more than 1 m, and even more so towards trees (≥ 10 m), which can have more dramatic effects on ecosystem properties (Lamarque *et al.*, 2011). Middle and high (Neartic, Antarctic and Paleatic) latitudes are also overrepresented compared to low latitudes with Neotropical, Oceanian, Afrotropical and Indomalayan biogeographical regions underrepresented (Figure 14a). Temperate and tropical biomes and ecosystems exhibit vastly different functioning regimes in terms of nutrient cycling dynamics (e.g. González and Seastedt 2001) as well as trophic interactions (Dyer & Coley, 2009). For instance, decomposition rates and the role played by the soil fauna in this process differs while there are increased levels of herbivory and diversity among herbivores in tropical regions. Due to these differences, it appears that our conclusion apply more to temperate and high latitude ecosystems than tropical ecosystems. Potential taxonomic biases in IAS families (Figure 14b) appear linked to this geographical bias in our dataset. Fagaceae, which appear to be overrepresented in our database, are mainly found in Neartic and Palearctic biogeographical regions and far more rarely in Neotropical and Oceanian regions. Similarly, all Balsaminaceae in the CABI database, and in our study, belong to the genus *Impatiens* that, while found natively in the tropics and subtropics of the Old World, has been documented as invasive mostly in Nearctic and Palearctic regions. As mentioned in the results, the overrepresentation of Simaroubaceae is caused by the numerous studies on the tree-of-heaven, *Ailanthus altissima*. These sources of bias do not invalidate, in our view, the overall results of this study. They should however be kept in mind when evaluating the results of this study and, most importantly, in applying these conclusions to geographical and climatic contexts that are underrepresented here.

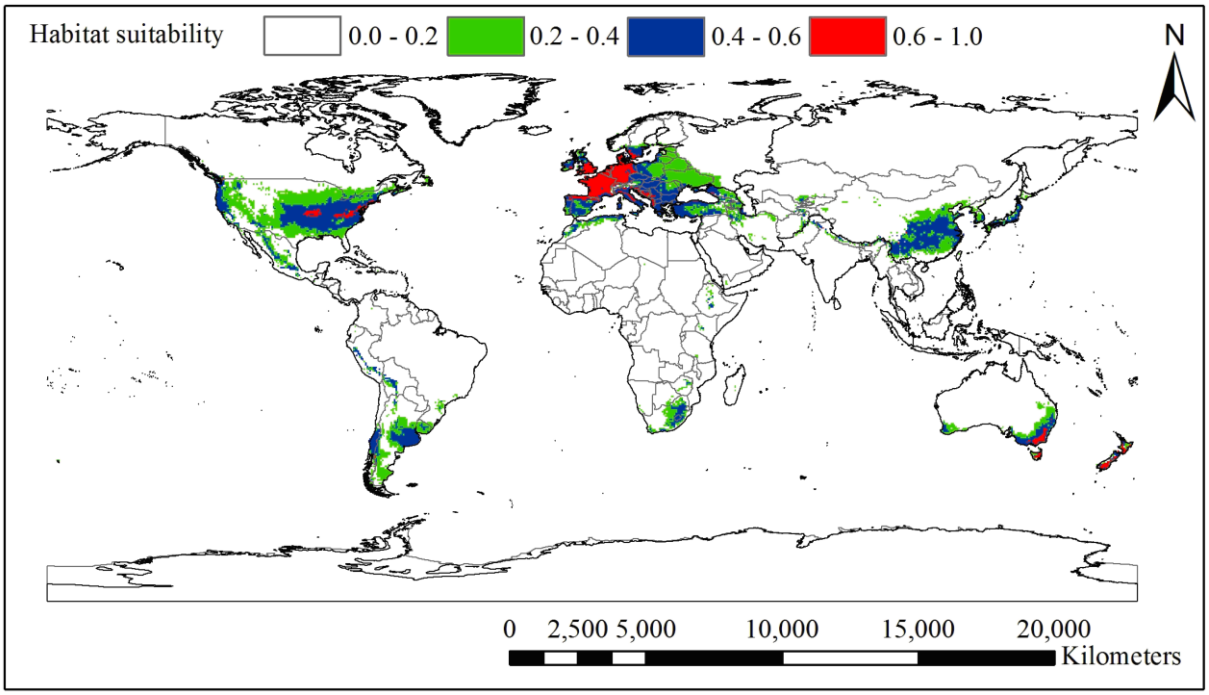
## 5. Conclusion and perspectives

This meta-analysis was an attempt to synthetize IAS effects on major soil trophic groups through meta-analysis, which enabled us to depict new and general patterns in soil fauna abundances following invasions. We showed that there was no overall pattern of response to IAS for the soil fauna contrary to the clearer trend of response of native plants to IAS in the literature (Hejda *et al.*, 2009; Pyšek *et al.*, 2012). In addition, we showed that the effect of invasive plants on the soil fauna is strongly dependent on habitat type with inverse trends in response between closed (positive effect) and open habitats (neutral effect). Trophic, and level within a food web, were also strong moderators of soil fauna responses. Our results confirm the importance of these two moderators in understanding

biological invasions as exemplified by other authors (McCary *et al.*, 2016). Despite these important results on the disruptive effect of invasive plants, the mechanisms underlying their responses to IAS remain unclear in many cases. The growing data available on the soil fauna compartment in invasion ecology will be essential in providing this understanding (Bardgett and Wardle 2010, see Figure 14d).

A number of explanations for this invasion success and effect on ecosystems have been proposed, such as enemy release hypothesis (ERH), superior competitor, novel weapons hypothesis (i.e. allelopathy; NWH), evolution of increased competitive ability (EICA), etc. (Catford *et al.*, 2009; Lowry *et al.*, 2013). We did not test these hypotheses in this meta-analysis yet this is a current focus in invasion biology, which needs to be further explored. Allelopathy and the novel weapons hypothesis are of particular interest regarding the interaction between invasive plants and the soil fauna (e.g Abgrall *et al.* 2018). We also highlighted the relative lack of knowledge on belowground predators trophic preference, which meant we could not assign them to a particular trophic pathway. Furthermore, invasive plant species functional traits should probably be considered for further synthesis. Both morphological and physiological traits may provide new mechanistic understanding of IAS effects on the soil fauna. There is however a need for more primary studies on this matter before a synthesis can be considered.

# Chapitre 2 – L'effet du robinier faux-acacia (*Robinia pseudoacacia*) sur la végétation native, le cycle de l'azote et les microarthropodes le long d'un gradient latitudinal Ouest-Européen




**Distribution potentielle globale du Robinia faux-acacia en fonction du climat**

Li *et al.* (2014). Mapping the global potential geographical distribution of black locust (*Robinia pseudoacacia* L.) using herbarium data and a maximum entropy model. *Forests*, 5(11), 2773–2792. doi: 10.3390/f5112773

# *Robinia pseudoacacia*: effect on native vegetation, nitrogen cycling and soil microarthropods along a West European climate gradient

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*In preparation*

## Abstract

Exotic alien species, such as black locust (*Robinia pseudoacacia*; Fabaceae), are a source of increasing concern among anthropogenic global changes due to their propensity to become invasive and their frequent negative environmental effects on native plant communities, nutrient cycling and arthropod communities. Most studies on such species are done on a limited number of sites and meta-analysis is used to extract generalizable results. Multi-site studies across invaded ranges are complementary to this approach by enabling generalization with homogeneous methodologies. Moreover, multi-site studies at larger scale can consider a wider range of pedological and climatic contexts. Here we conducted a multi-site study on the impacts of replacement, partial (i.e. mixed) or total, of native tree species (here, various locally dominant *Quercus* species) by *R. pseudoacacia* across a latitudinal gradient in Western Europe, from Wallonia in Belgium to Catalonia in Spain. We sampled the soil and measured standard and specific properties notably related to nitrogen-cycling as *R. pseudoacacia* is a N-fixer. We also sampled understory plant communities, soil microarthropods and nematodes. At large-scales, increased *R. pseudoacacia* cover favoured increased total nitrogen and nitrate content, reduced organic layer depth and lowered soil pH. Contrary to what is frequently suggested in the literature there was no decrease in native understory plant diversity under *R.pseudoacacia* although there was an increase in total cover. There was a quadratic relation between plant diversity and *R. pseudoacacia* cover with a higher diversity in mixed plots compared to both *Quercus* sp. or *R. pseudoacacia* plots. There were few changes within soil fauna communities (microarthropods and nematodes) in relation to the presence of *R. pseudoacacia*. These general results differed substantially between regions, frequently between southern and northern sites, and highlight that generalization of site-specific results on the effect of exotic species should be done with caution.

*Keywords:* plant-soil interactions; global changes; biotic interactions; soil trophic groups; invasive alien species (IAS); soil communities; exotic tree; collembola; acari; biological invasions

## 1. Introduction

Numerous exotic species become invasive and alter the structure and functioning of invaded native ecosystems with repercussions on native plant and fauna communities (Vilà *et al.*, 2011; Pyšek *et al.*, 2012). Biological invasions are a global change facilitated by others such as land-use change (Hill *et al.*, 2005) and expected to be amplified by the perturbations caused by climate change (Dukes & Mooney, 1999). Large scale analysis of the repercussions of invasive species frequently involve meta-analysis based on multiple independent studies (e.g. McCary *et al.* 2016, Zhang *et al.* 2018). Few have focused on a single exotic species and their impact at large spatial scales with the same methodology (Weidenhamer & Callaway, 2010; Kramer *et al.*, 2012). Invaders have large ranges frequently encompassing thousands of square kilometres, with their potential impact similarly broad and diverse, as the invaded areas (Pyšek *et al.*, 2012). In fact, there appears to be a negative relationship between the spatial extent of studies on plant invasion impacts and the effect size of their impact on native vegetation (Gaertner *et al.*, 2009; Powell *et al.*, 2011). This makes multi-site studies complementary to meta-analysis (MacDougall *et al.*, 2006; Gerber *et al.*, 2008; Kramer *et al.*, 2012).

The black locust (*Robinia pseudoacacia* L.) is an exotic, frequently invasive, leguminous tree native to North America and introduced in Europe in the 16$^{th}$ century (Li *et al.*, 2014) and has since been widely planted where it has frequently escaped and become invasive (Keresztesi, 1988). Through association with nitrogen-fixing bacteria, it has the ability to grow in nitrogen-limited conditions where other species would not (Franche *et al.*, 2009). As a result *R. pseudoacacia* leafs exhibit a higher nitrogen content than most natives (Medina-villar *et al.*, 2015) as well as other traits linked to early-successional stages competitive ability (Grotkopp & Rejmánek, 2007). These traits, which favour *R. pseudoacacia* as a pioneer species, can also be responsible in many cases for altered ecosystem functioning (Medina-Villar *et al.*, 2015), notably nitrogen-cycling (Rice *et al.*, 2004; Landgraf *et al.*, 2005), and repercussions on native plant communities (Peloquin & Hiebert, 1999; Rice *et al.*, 2004; Benesperi *et al.*, 2012; Kou *et al.*, 2016) and soil organisms (Degomez & Wagner, 2001; Brygadyrenko, 2015; Della Rocca *et al.*, 2016; Schirmel *et al.*, 2016). Plant diversity in temperate forests seems less impacted than open habitats in other biomes (Gaertner *et al.*, 2009; Pyšek *et al.*, 2012) while the opposite would be true for animals (McCary *et al.*, 2016). As *R. pseudoacacia* is generally found to increase soil nitrogen (e.g. Rice *et al.* 2004), a limiting factor in temperate forests, we hypothesized that increased *R. pseudoacacia* cover would favour increased plant biomass and cover.

Western Europe has been shown to have nearly optimal habitat suitability for the implantation of *R. pseudoacacia* in terms of temperature (5.8-14.5 °C optimum) and precipitations (508-1867 mm optimum) (Li *et al.*, 2014). The same global model also showed that they are strongly constrained by

excessively cold temperatures during the non-growing season (i.e. that can negatively influence fruit maturation, which occurs in late autumn) and high temperatures during the early growth season (i.e. that can suppress leafing and flowering). Flower litter from *R. pseudoacacia* represents a significant amount of high-quality litter input during spring and early summer (6% of annual input; Medina-Villar *et al.* 2015) with the date of flowering strongly influenced by temperature (Walkovszky, 1998). Changes in litter quality and seasonality could be expected to have repercussions on soil functioning (Medina-Villar *et al.*, 2015, 2016) and soil animals (Degomez & Wagner, 2001; Brygadyrenko, 2015; Buchholz *et al.*, 2015; Della Rocca *et al.*, 2016).

We wanted to assess how differences in climate, and spatial scale, may affect the response of native plants, the soil fauna and their substrate to replacement of native tree species by *R. pseudoacacia*. We hypothesized (i) that soil properties would be affected by the presence of *R. pseudoacacia* with the strongest effect on nitrogen-cycling, (ii) that native understory plant species richness and diversity would be negatively affected by the presence of *R. pseudoacacia,* (iii) that soil fauna (micro- and mesofaunal) communities structure would change in response to *R. pseudoacia* through induced changes in soil properties and understory plant communities. We conducted a large-scale study along a latitudinal gradient across Western Europe to test these hypotheses.

## 2. Material & Methods

### ***2.1. Study sites & experimental design***

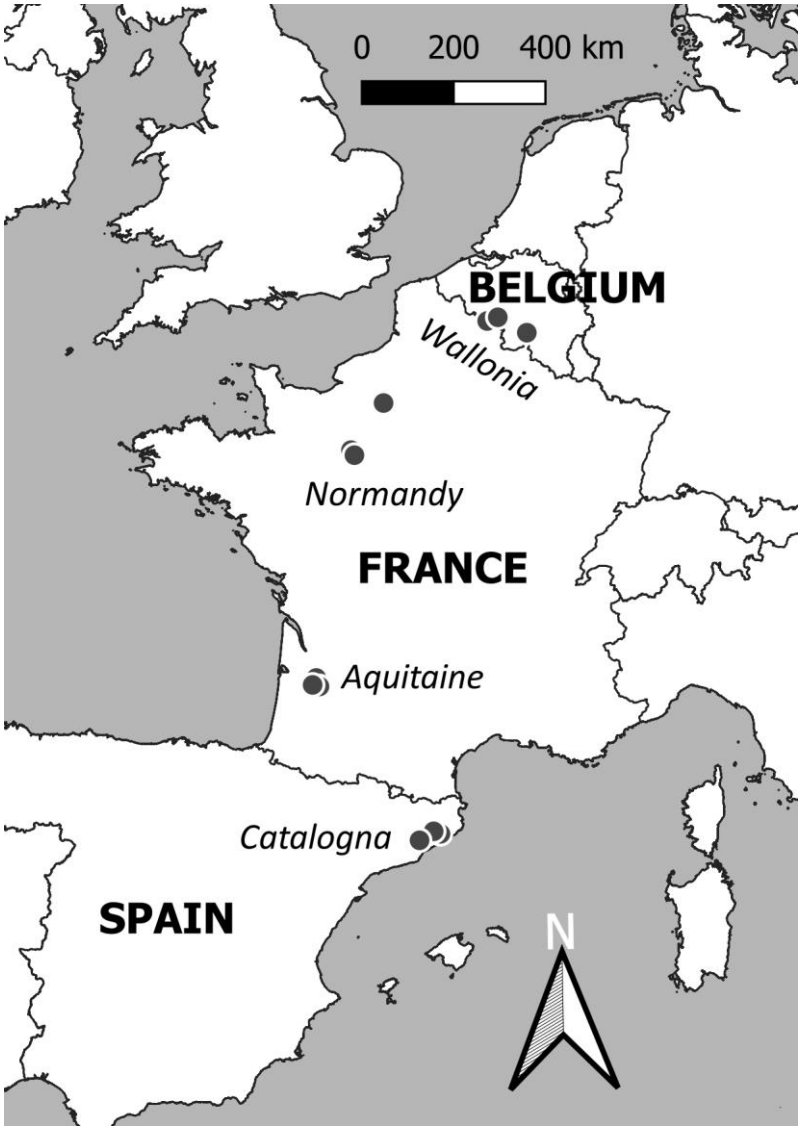


*Figure 16: Map of Robinia pseudoacacia study sites in Western Europe in four distinct regions: Catalonia in Spain, Aquitaine and Normandy in France and Wallonia in Belgium. Dots are the study sites and include three types of plots (i.e. modalities): Quercus sp. dominated, R. pseudoacacia dominated and mixed plots with three pseudo-replicates for each modalities.*

We sampled *R. pseudoacia* and native *Quercus* sp. plots in 4 distinct regions accross Western Europe: Catalonia in North-Eastern Spain, Aquitaine in South-Western France, Normandy in North-Western France and Wallonia in South-Eastern Belgium (Figure 16 & Table 4). Catalonia has a hot-summer Mediterranean climate (Csa on the Köppen-Geiger climate classification) while the other three have a temperate oceanic climate (Cfb) with differences in annual temperatures, precipitations and annual sunshine hours (Table 4). Dominant soil types were Calcisols/Cambisols in Catalonia, Luvisols in Aquitaine and Wallonia and Luvisols/Calcisols in Normandy (Jones *et al.*, 2012). Native controls were the evergreen oak in Catalonia (*Quercus ilex* L.) with occasional presence of cork oak (*Quercus suber* L.), the downy oak in Aquitaine (*Quercus pubescens* Willd.), the sessile oak in Normandy (*Quercus petrea* (Matt.) Liebl.) with, possibly, some hybrids and the common oak (*Quercus robur* L.) in Wallonia.

In each region, we selected 3 distinct forest areas (i.e. sites) as replicates. At each site, we picked close-by sampling areas (i.e. plots) per modality: native dominated, *R. pseudoacia* dominated and a mixed plot with both species in roughly equal densities for a total of 108 plots sampled (4 regions × 3 sites × 3 modalities × 3 sampling units). We sampled the soil, the understory vegetation and the soil fauna in within a single week in each region between mid-April and early June 2017 (Table 4).

*Table 4: Details on study sites used in this study. Temperatures and precipitation are segregated according to proxmitiy. Csa: climat méditerranéen à été chaud; Cfb: climat océanique tempéré.*

| *Region* | *Site name* | *Native control* | *Sampling date* | *Geography & Topography* | | | *Dominant soil type* | *Köppen-Geiger classif.* | *Temperature* | | | *Average precipita-tions (mm)* | *Mean annual sunshine hours* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Latitude* | *Longitude* | *Elevation* | | | *Avg. Low* | *Avg. High* | *Mean annual* | | |
| Catalogna | Sant Feliu | *Quercus ilex* | 17th - 22nd April | 41.788 | 2.572 | 325 | Calcisol | Csa | 8.6 | 20.8 | 14.7 | 698.2 | 2295.8 |
| | Arbuçies | | | 41.833 | 2.507 | 375 | | | | | | | |
| | Els Saulons | | | 41.670 | 2.165 | 422 | Cambis. | | 15.1 | 21.2 | 18.2 | 571.9 | 2524.7 |
| Aquitaine | Uzeste | *Quercus pubescens* | 01st - 06th May | 44.447 | -0.341 | 68 | Luvisol | Cfb | 8.4 | 18.5 | 13.4 | 916.9 | 1908.4 |
| | Préchac | | | 44.401 | -0.334 | 45 | | | | | | | |
| | Villandraut | | | 44.427 | -0.370 | 31 | | | | | | | |
| Normandy | Mélarbière | *Quercus petraea* | 15th - 20th May | 48.356 | 0.500 | 177 | Calcisol | Cfb | 6.6 | 15.3 | 11.0 | 746.7 | 1689.5 |
| | Pouvrai | | | 48.276 | 0.525 | 145 | | | | | | | |
| | Autheuil | | | 49.111 | 1.292 | 83 | Luvisol | | 6.6 | 15.0 | 10.8 | 604.6 | 1684.4 |
| Wallonia | Petit Hornu | *Quercus robur* | 29th May - 03rd June | 50.398 | 3.806 | 93 | Luvisol | Cfb | 2.1 | 17.5 | 10.2 | 781.2 | 1621.3 |
| | Boussolt | | | 50.456 | 4.064 | 67 | | | | | | | |
| | Morville | | | 50.217 | 4.768 | 160 | | | 1.7 | 17.4 | 10.0 | 819.4 | 1542.2 |

### *2.2. Sampling*

At each sampling unit we measured the depth of the holorganic layer and collected composite soil samples from the top 10 cm of the organo-mineral (A) layer using steel soil corers (⌀ 5 cm). These cores were pooled and used for soil measurements. The same soil corers were used to collect two more cores: one for soil nematodes and one for soil micro-arthropods (collembola and acari) from the holorganic layer and the organo-mineral layer. Samples were then separated into O and A fractions for transportation and extraction. Soil samples were kept in polyethylene bags and in refrigerated chest coolers for transportation from field sites to the laboratory or a temporary storage fridge. We used special purpose stainless steel cylinders (⌀ 5 cm, 100 $cm^3$) to sample the organo-mineral layer in order to measure bulk density. Each cylinder was then closed at both ends with plastic caps and transported to the laboratory

Understory plant communities were sampled prior to soil sampling using the Braun-Blanquet cover-abundance scale in 2 × 2 m area and local or West-European identification keys and floral guides. We measured canopy openness above the sampling unit using a standard high-res digital camera facing south at a 20° angle perpendicular to the soil surface and used it to assess understory light availability.

### *2.3. Soil properties measurements*

Upon return to the laboratory we used a Berlese-Tullgren funnel for microarthropod extraction and a modified Baermann funnel for nematode extraction. One core was used for microarthropod extraction and one for microfaunal. Microarthropods samples were separated while in 70% ethanol into Acari and Collembola under a stereo binocular microscope. We then counted the number of gamasid and oribatid acari from the previously separated sample. Regarding collembola, we counted individuals according to eco-morphological groups: epiedaphic, hemiedaphic and euedaphic.

Upon return to the laboratory soil samples were subdivided into two fractions: "fresh", to be kept refrigerated during the days separating sampling from measurements, and "dry" to be air-dried prior to later measurements. The fresh soil fraction was used to measure relative humidity, ergosterol content, total organic carbon (before and after fumigation) as well as measure mineral nitrogen (nitrate and ammonium). Once dried, the dry fraction was used to measure soil pH as well as total nitrogen and carbon content.

Relative humidity was calculated by weighting the same soil sample (roughly 50 g) before and after 24h of oven drying at 105 °C. Fungal biomass was estimated using ergosterol content, a sterol found within fungi and protozoa, and the method proposed by Gong, Guan & Witter (2001). Four grams of fresh soil were used to mechanically (glass beads) and chemically (methanol) extract

ergosterol from the soil. Ergosterol content was then measured using high-performance liquid chromatography (ThermoFisher Scientific UltiMate 3000 UHPLC) and a commercially available ergosterol solution. Microbial biomass was estimated using the chloroform ($CH_3Cl$) fumigation-extraction method (Voroney *et al.*, 2008). Two 20 g samples of fresh soil were extracted, either with or without a 24h $CH_3Cl$ fumigation in a vacuum chamber, in 100 ml of a 0.2 M potassium sulphate ($K_2SO_4$) solution. Total organic carbon was measured in both samples using the NPOC method in a Shimadzu TOC-L Total Organic Carbon Analyzer. Soil mineral nitrogen content was evaluated by measuring nitrate ($NO_3^-$) and ammonium ($NH_4^+$) content following extraction of 20 g of soil in 100 ml of 0.2 M NaOH and using a ThermoFisher Gallery Automatic Sequential Analyzer.

Using dried soil samples we measured pH using 10 g of soil diluted in 25 ml of ultrapure water (i.e. Milli-Q) or a 1:2.5 mass to volume ratio (Hendershot *et al.*, 1993). Measurements were carried out after 30 min of intermittent stirring and 1 h of decantation. Total carbon and nitrogen were measured using the Dumas method and precisely weighted 50 ± 0.05 mg dry soil samples in a ThermoFisher Flash Analyzer 2000.

We used the specially collected soil cores (100 $cm^3$) to evaluate bulk density (Hao *et al.*, 2008). These samples were dried at 105 °C for 24 h in an oven. The dry mass of the soil divided by the cylinder volume, after removing the mass and volume of coarse elements (i.e. rocks and root debris) from the calculation, gave the bulk density in $g.cm^3$.

### *2.4. Statistical analysis*

We used redundancy analysis (RDA) to visualize and separate the effects of latitude (and *Quercus* species) and *R. pseudoacacia* cover on soil properties and microbiological variables. In RDA, the components from **Y** (i.e. matrix of environmental variables) are extracted so as to be as correlated as possible to **X** (i.e. matrix of latitude and *R. pseudoacacia* canopy cover) using unweighted linear regression and singular value decomposition. This reveals the influence of variables within **Y** on those within **Y** in an operation known as "constraining" which, here, shows the response of environmental variables to the presence or dominance of exotic and native tree species. Constraining, and its elements, can be quantified by a permutation test (differences in residual deviance in permutations of nested models) thus enabling a rough indication of the components of variance within **Y** based on **X**.

Following this more general approach, we considered soil variables most frequently reported to differ between *R. pseudoacacia* plots, an exotic N-fixer, and native control: total carbon to nitrogen ratio and nitrate concentration (Rice *et al.*, 2004; Landgraf *et al.*, 2005). We also included organic layer

depth due to its drastic and rather unexpectedly strong response. We used ANOVA per region to show differences between modalities for these soil variables.

For plant communities where we had species-level identification we computed species richness and Shannon's diversity. We plotted these indices by region (Catalonia, Aquitaine, Normandy and Wallonia) and modality (*Quercus*-dominated, mixed and *Robinia*-dominated) using barplots. We used ANOVA to check for the existence of differences between modalities per region and Tukey's tests to identify these differences. We tested the positive effect of *R. pseudoacacia* cover (and possible positive effect on soil nitrogen) using linear regression ($y = ax + b$) and displayed these regressions with their confidence intervals on scatterplot of indices by *R. pseudoacacia* cover. *R. pseudoacacia* has often been found to decrease understory plant species richness and diversity (Peloquin & Hiebert, 1999; Rice *et al.*, 2004; Benesperi *et al.*, 2012; Kou *et al.*, 2016) although this is not always the case (Akatov *et al.*, 2012; Sitzia *et al.*, 2012; Masaka *et al.*, 2013; Von Holle *et al.*, 2013). On the other hand, understory plant diversity has often been found to be positively correlated to tree diversity (Mölder *et al.*, 2008; Vockenhuber *et al.*, 2011) although not always (Aubert *et al.*, 2004) in which case mixed plots could have a comparatively higher species richness and diversity than control plots despite the presence of *R. pseudoacacia*. As plant species richness and diversity could be expected to decrease or remain the same in *R. pseudoacacia* plots and increase or remain the same in mixed plots we tested this hypothesis using polynomial regression ($y = ax^2 + bx + c$) along a *R. pseudoacacia* cover gradient.

Finally, we wanted to test the effect of the presence of *R. pseudoacacia*, latitude as well as soil properties on the soil fauna. Soil variables selected as biologically susceptible to influence the soil fauna were canopy openness which can lead to dessicative stress, bulk density which is correlated to porosity and thus ease of displacement within the soil, pH which can constrain soil organisms for example through sorption of heavy metal, fungal and microbial biomass as fungi and bacteria are a primary trophic resource for most nematodes and springtails as well as many acari and finally several indices of plant communities: cover, richness and diversity which can influence the soil fauna trophically and various other mechanisms We used the same method (RDA) as with soil variables with the aforementioned variables as constraints. We used permutation tests to assess the significance, or lack thereof, of the effect of each variable on the soil fauna as a whole. We plotted the results in order to reveal differentiated responses between soil fauna groups.

All statistical analysis was performed using the open source statistical software R version 3.5.2 (2018-12-20) (R Core Team, 2018). RDAs were computed using the `rda()` function from package vegan version 2.5.3 (Oksanen *et al.*, 2019).

## 3. Results

### *3.1. Soil properties*

The RDA of soil properties constrained by latitude and *R.pseudoacacia* canopy cover revealed that the former explained a much higher fraction of the variability than the later (26.8 % and 4.1 %, respectively; Figure 17). The first RDA axis (86.8 % of constrained variance) shows a distinction among soil properties based on latitude. Considering that sites are clumped together per region the variable can be considered to be a "region effect". Moreover, since we had to consider different native *Quercus* species as control per region the effect also accounts for differences between these species. Total soil carbon and nitrogen content as well as nitrate content increased with latitude while microbial and fungal biomass (i.e. fumigation-extractible carbon and ergosterol content), canopy openness and bulk density decreased with latitude. The second RDA axis (13.2 % of constrained variance) shows a distinction between sites dominated by *R. pseudoacacia* and those dominated by native *Quercus* species. *R. pseudoacacia* cover was positively correlated to soil bulk density and nitrate content and negatively correlated to organic layer depth and soil pH.

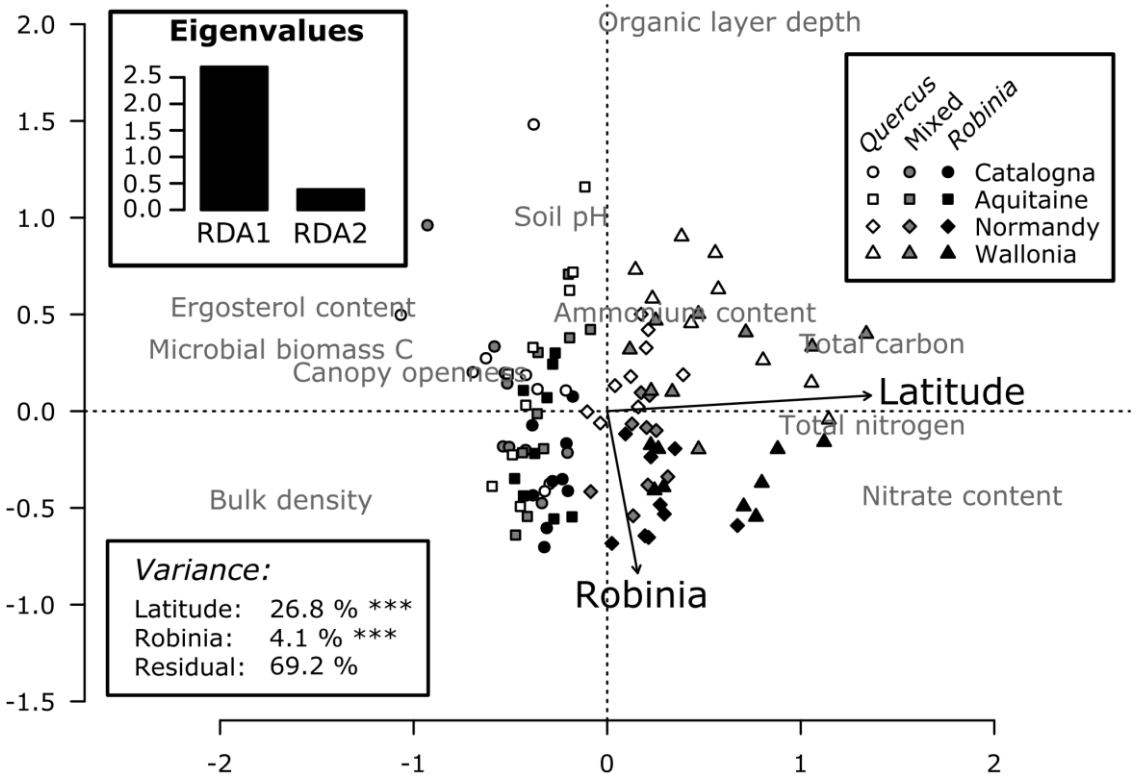


*Figure 17: Redundancy analysis (RDA) biplot of soil properties and environmental variables as constrained by the latitude [41.67-50.46 °N] of the study site and Robinia pseudoacacia cover [0-100%]. Black arrows and text show how soil properties and environmental variables are constrained by latitude and cover. Light grey text shows the result of principal components analysis (PCA) on soil properties and environmental variables after constraining while coloured symbols are individual sampling points differentiated by modality and region. n.s.: p > 0.05, * : p < 0.05, ** : p < 0.01, *** : p < 0.001, **** : p < 0.0001*

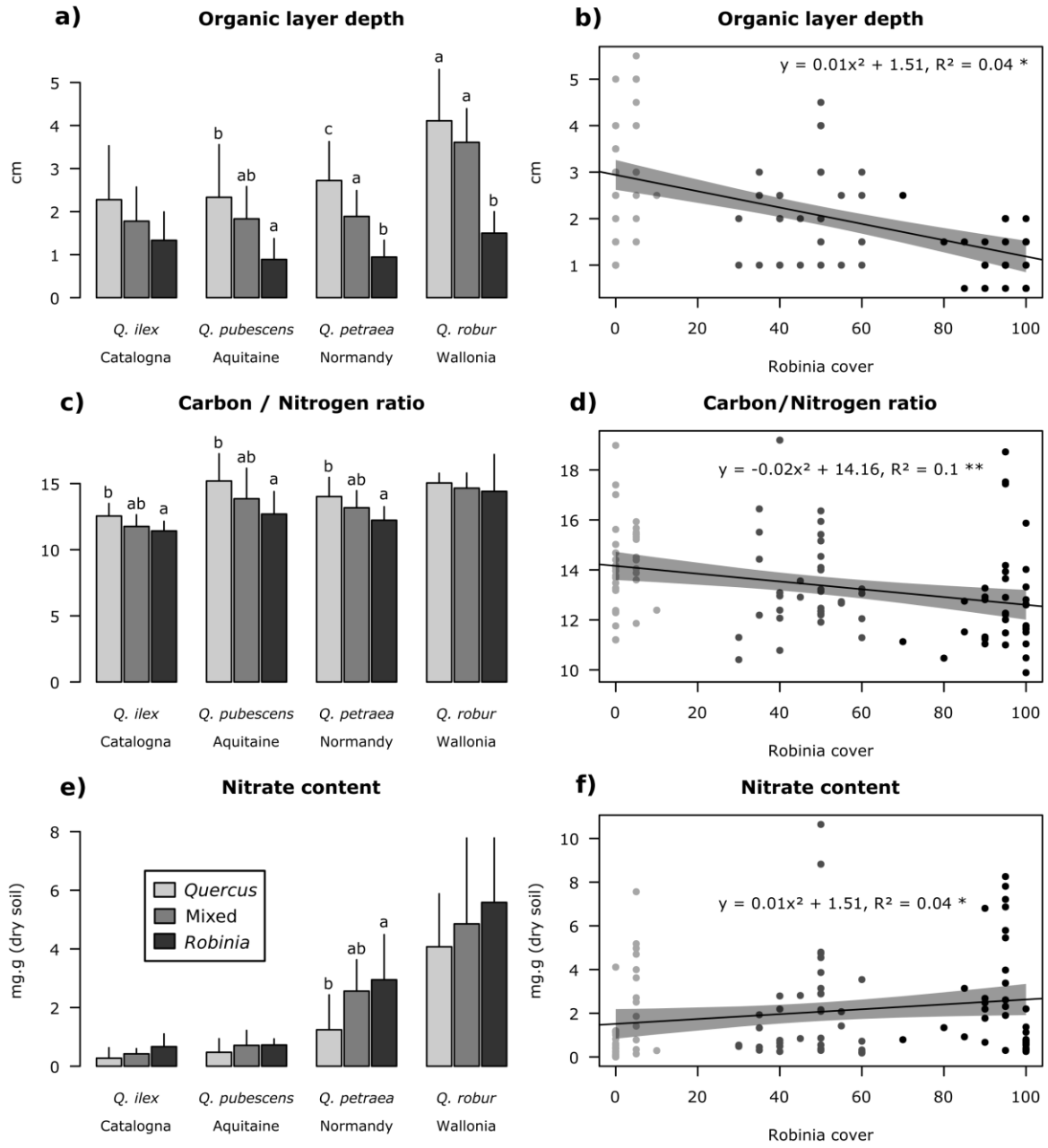


*Figure 18: Barplots and scatterplots of soil properties purported to be influenced by R. pseudoacacia and/or found to be affected in our study. Values for barplots (a, c, e) are means and standard deviations by region and modality for soil properties. Black boxes are R. pseudoacacia plots, dark grey boxes are mixed plots and light grey boxes are control Quercus sp. plots. Letters, when displayed, indicate that significant differences were found by ANOVA between modalities across a particular region. The letters themselves are a result of a Tukey post-hoc test. For scatterplots (b, d, f) different colours illustrate how assigned modalities are related to R. pseudoacacia cover, lines are linear regression lines (y = ax + b) of soil variables by Robinia cover by R. pseudoacacia cover and shaded polygons represent confidence intervals (α = 0.05) of the regression line.*

The main changes were a reduction in organic layer depth ($R^2 = 0.30$, $p < 0.05$; Figure 18b) and a very small decrease in soil pH ($R^2 = 0.06$, $p = 0.008$). We found decreased organic layer depth under *R. pseudoacacia* in Aquitaine ($F = 6.32$, $p = 0.006$), Normandy ($F = 16.02$, $p < 0.001$) and Wallonia ($F = 22.7$, $p < 0.001$) with intermediate depths in mixed plots (Figure 18a). Soil properties related to nitrogen cycling for which we hypothesized a strong response to *R. pseudoacacia* were less affected at large scales than expected. Two-factor ANOVA analysis showed that soil nitrate content, for instance, was influenced to much higher degree by latitude ($F = 120.11$, $p < 0.001$) compared to *R. pseudoacacia* cover ($F = 8.61$, $p = 0.04$). Nevertheless, soil nitrate content did increase under *R. pseudoacacia* at the broadest of scale. Southern sites (Catalonia and Aquitaine) were unaffected while nitrate increased under *R. pseudoacacia* in northern sites (Normandy and, to a lesser insignificant extent, Wallonia). At smaller scales, nitrate content differed significantly in Normandy only ($F = 4.37$, $p = 0.024$; Figure 18e). There were also changes in soil carbon to nitrogen ratio in most sites with a decrease found in Catalonia ($F = 4.08$, $p = 0.030$), Aquitaine ($F = 3.489$, $p = 0.047$) and Normandy ($F = 4.501$, $p = 0.022$) but not in Wallonia (Figure 18c). As mentioned above when including all regions and sites *R. pseudoacacia* cover did improve nitrate content, albeit marginally.

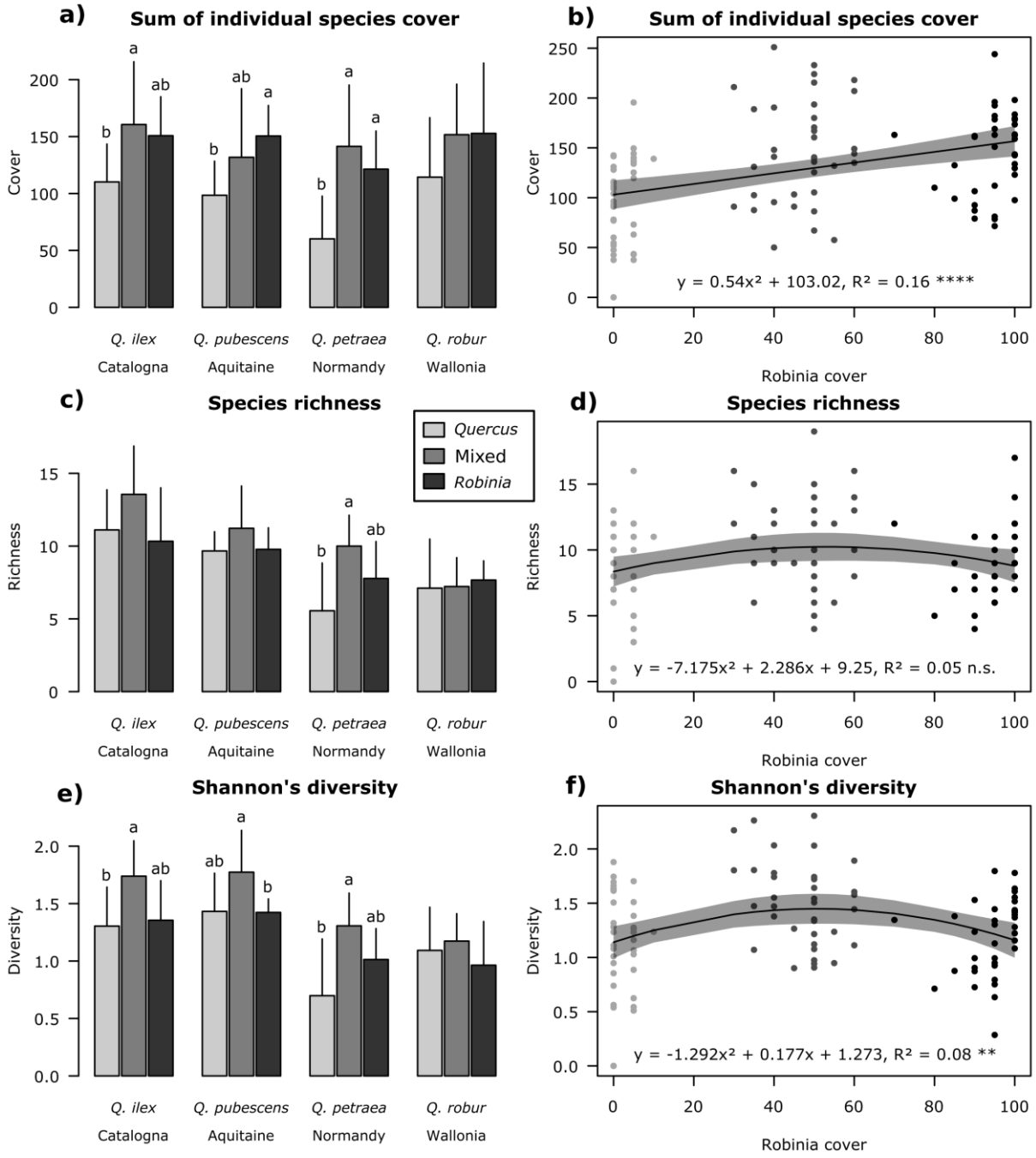


*Figure 19: Barplots and scatterplots of understory plant community indices (plant cover, species richness and diversity) by regions and modalities (barplots) or quantitative R. pseudocacacia cover (scatterplots). For barplots (a, c, e) different letters indicate significant differences between modalities within a particular region as determined by a Tukey's test after ANOVA. For scatterplots (b, d, f) different colours illustrate how assigned modalities are related to R. pseudoacacia cover, lines are polynomial ($y = ax^2 + bx + c$) or linear ($y = ax + b$) regression of indices by R. pseudoacacia cover and shaded polygons represent confidence intervals ($\alpha = 0.05$) of the regression line.*

### ***3.2. Understory vegetation***

We found significant difference in understory plant total cover between control and *R. pseudoacacia* plots in Aquitaine ($F = 3.58$, $p = 0.044$) and Normandy ($F = 8.90$, $p = 0.001$) where plant cover increased under *R. pseudoacacia* and, in Normandy, under mixed plots as well (Figure 19a). In Catalonia there were only differences between control and mixed plots ($F = 3.62$, $p = 0.042$) with an insignificant increase in *R. pseudoacacia* plots. There were no change in vegetation cover in Wallonia ($F = 1.52$, $p = 0.240$). Regarding plant species richness the only difference found was in Normandy where species richness increased in mixed plots, but not in *R. pseudoacacia* plots, compared to control values ($F = 6.14$, $p = 0.007$, Figure 19c). Plant diversity was not affected by *R. pseudoacacia* dominance in any region (Figure 19e) yet increased in mixed plots in Catalonia ($F = 4.64$, $p = 0.020$) and Normandy ($F = 6.27$, $p = 0.006$) compared to control. In Aquitaine the only difference was between mixed and *R. pseudoacacia* plots with mixed plots having a higher plant diversity ($F = 4.19$, $p = 0.026$). There was no difference in understory plant diversity between modalities in Wallonia ($F = 0.86$, $p = 0.426$).

We found increased understory plant cover in relation to increased *R. pseudoacacia* cover across all sites along the latitudinal gradient ($F = 20.52$; Figure 19b). Latitude itself had no effect plant cover ($F = 0.65$, $p = 0.428$). We found no relation between species richness and *R. pseudoacacia* cover ($F = 2.69$; Figure 19d) while latitude itself had a significant and negative effect on species richness ($F = 40.75$, $p < 0.0001$). Conversely, there was a week quadratic relation between understory plant diversity and *R. pseudoacacia* cover ($F = 4.84$; Figure 19f) although latitude had a much stronger linear effect ($F = 44.04$, $p < 0.001$). As plots with intermediate *R. pseudoacacia* cover are mixed with *Quercus* sp. this relationship can be construed as indicating a positive effect of tree species diversity.

### 3.3. Soil fauna

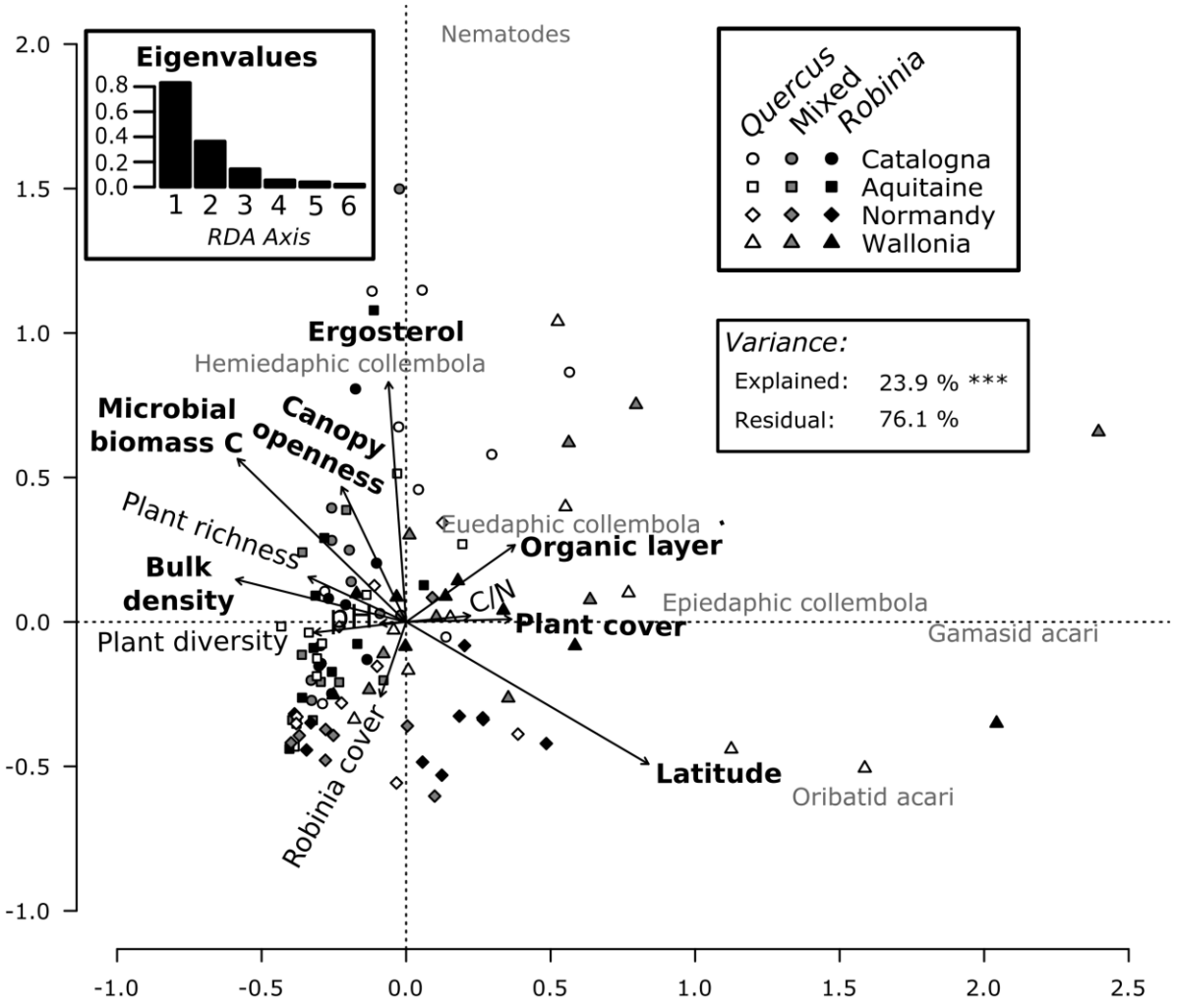


*Figure 20: Redundancy analysis (RDA) biplot of soil fauna taxonomic or eco-morphological groups abundances as constrained by the latitude [41.67 - 50.46 °N] of the study site, Robinia pseudoacacia cover [0 - 100%] as well as biologically relevant soil properties and environmental variables. Black arrows and text show how soil fauna group abundances are constrained by latitude, cover and soil properties. Bold text indicate a significant effect on the soil fauna as a whole by the considered variable while normal text show variables with no effect. Text elements were moved for clarity and coordinates should be read from arrow tips. Light grey text shows the result of principal components analysis (PCA) soil fauna group abundances after constraining while coloured symbols are individual sampling points differentiated by modality and region. n.s.: p > 0.05, * : p < 0.05, ** : p < 0.01, *** : p < 0.001, **** : p < 0.0001*

Robinia cover combined with latitude as well as floral communities and soil properties explained 23.9 % of the variance within soil fauna communities (Figure 20). *R. pseudoacacia* cover had no influence on soil fauna communities ($F = 0.92$, $p = 0.45$) while latitude did ($F = 2.92$, $p = 0.02$). Plant communities affected the soil fauna only through their cover ($F = 2.77$, $p = 0.032$) and not their species richness ($F = 1.48$, $p = 0.20$) or diversity ($F = 1.60$, $p = 0.18$). Regarding soil variables there was a strong effect of organic layer depth ($F = 5.4$, $p < 0.001$), fungal biomass ($F = 4.08$, $p < 0.01$) as well weaker effects of soil bulk density ($F = 2.91$, $p = 0.03$), canopy openness ($F = 2.88$, $p = 0.04$) and microbial biomass C ($F = 3.42$, $p = 0.01$) and no effect of soil pH ($F = 0.35$, $p = 0.87$) or soil C/N ratio ($F = 0.88$, $p = 0.48$).

The first RDA component, accounting for 58.0 % of constrained variability, shows a distinction between northern sites with increased plant cover, organic layer depth, lower soil bulk density, and decreased microbial biomass and southern sites where the reverse is true (Figure 20). These conditions favour increased abundance for acari (both gamasid and oribatid) and epiedaphic collembola and a limited increase in euedaphic collembola abundance. Conversely, the second RDA component, accounting for 25.6 % of constrained variability show a distinction between southern sites with high fungal and microbial biomass and open canopies and northern sites with opposite characteristics. These conditions favour increased nematode and hemiedaphic collembola abundances. *R. pseudoacacia* does not appear to alter soil fauna communities at least in terms of abundance.

## 4. Discussion

We found that plots with *R. pseudoacacia* showed relatively little difference with the control plots across spatial scales as latitude appeared as the primary driver of changes (4.1% vs 26.8% of explained variance within soil variables, for example). The main broad-scale changes within soil properties were a reduction in organic layer depth and a very small decrease in soil pH. Nitrogen related variables were far less impacted than hypothesized, or then suggested by the literature. Total nitrogen and ammonium were only affected in Normandy, positively in the first two cases and negatively in the latter. Nitrate content was positively correlated, albeit weakly, to *R. pseudoacacia* cover. There was also an increase in total nitrogen and nitrate with latitude, which was not found with ammonium. Plant communities were positively affected in their total cover by *R. pseudoacacia,* although once again with differences depending on the considered region, while species richness and diversity were unaffected independently of the considered scale. We found increased plant diversity in mixed plots compared to both controls and *R. pseudoacacia* plots. The soil microfauna (i.e. nematodes) and mesofaune (i.e. acari and collembola) were impacted by latitude but largely unaffected by the presence of *R. pseudoacacia* with the exception of euedaphic collembola in Catalonia. Overall, and despite changes in soil properties, the presence of *R. pseudoacia* had limited repercussions on floral and faunal communities.

### *4.1. The soil and nitrogen*

As suggested by the literature (e.g. Rice *et al.* 2004, Medina-Villar *et al.* 2016) we hypothesized that, due to its differences from native counterparts (including nitrogen-fixation) and pioneer characteristics, *R. pseudoacacia* would affect ecosystem functioning even at large scales. Our results highlight some large-scale trends, such as a small overall increase in soil nitrate content and pH, or the drastic change in organic layer depth. Most results show limited and context-dependent effect, though.

Soil nitrogen, both organic mineral, has been found to increase under *R. pseudoacacia* compared to native ecosystems (Rice *et al.*, 2004; Landgraf *et al.*, 2005; Taniguchi *et al.*, 2009; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2015). We did find a small increase in soil nitrate content as well as a decrease in soil total carbon to total nitrogen ratio with increasing *R. pseudoacacia* coverage. However while this pattern is true at a large scale increased total nitrogen and nitrate was only confirmed separately within Norman sites (Figure 18b). There were, however, decreases in soil C/N ratio in most regions, with the exception of Wallonia (Figure 18c). This increase is probably related to the rare, in temperate tree species, ability to fix atmospheric nitrogen through symbiotic association with Rhizobia. Yet, if that case, we would have expected a higher increase in nitrogen and nitrate content. For instance, Rice and collaborators (2004) found a two-fold increase in soil total nitrogen and

a ten-fold, or more, increase in soil nitrate content (compared to a pine-oak mixture). This same two-fold increase was found for total soil nitrogen in the A layer by Medina-Villar et al (2015) in Spain, Wang et al (2012) in China and Landgraf et al (2005) in Germany. In the latter case, soil nitrate content was also found to increase at least five-fold. Our findings show much lower variations in average values for both total nitrogen and nitrate content. This increased nitrogen content is probably the reason for the observed increase in soil pH.

Despite the aforementioned large-scale results there were considerable differences between regions in both absolute values for soil variables and relative differences between modalities. For instance, Norman and Walloon sites are relatively similar in terms of mean temperatures, precipitations as well as sunshine hours (Table 4), yet showed generally striking differences in response. In addition, the native control species (*Q. petraea* in Normandy and *Q. robur* in Wallonia) are relatively similar, at least functionally. In these regions, most variables had values more similar than to those in southern sites (Aquitaine and Catalonia) but that did not translate into similar responses to replacement by *R. pseudoacacia*. One striking case of this difference was for microbial biomass C for which a tenfold difference in average values was found between northern and southern sites yet with no effect of *R. pseudoacacia* cover in either case.

### *4.2. More of the same: increased plant cover but no change in diversity*

Based on the literature on *R. pseudoacacia*, and on nitrogen-fixing tree species in general, we expected understory vascular plant communities to be drastically affected by replacement of native species with *Robinia*.

Our main finding was an increase in understory plant cover under *R. pseudocacia* at latitudinal gradient scale (Figure 19b). When decomposing this response by region, however, this observation only held true in the two French sites, Aquitaine and Normandy, although a similar trend was found in Catalonia and Wallonia (Figure 19a). Mixed plots generally had values closer to, or above, those in *R. pseudoacacia* plots than in native *Quercus* sp. plots, suggesting multiple factors involved and not only *R. pseudoacacia* presence. *R. pseudoacacia* is nitrogen-fixing and reportedly increases soil nitrogen content, particularly assimilable mineral nitrogen (e.g. Rice *et al.* 2004, Landgraf *et al.* 2005). It would be fair to assume that increased plant cover would be linked to increased mineral nitrogen supply, as it is a key limiting factor to plant growth in temperate ecosystems (Franche *et al.*, 2009). Canopy openness, and thus available light, could also influence plant cover by increasing energy input to the understory (Von Holle *et al.*, 2006). However, canopy openness was unaffected by the presence of *R. pseudoacacia* in our study. Nitrate content did increase, very weakly, with *R. pseudoacacia* cover

across the whole gradient yet, at the regional scale, this was only significant in Normandy. Increased nitrate content can thus tentatively be considered the cause of this increase in plant cover.

The literature on the subject suggests decreased understory plant species richness, and diversity, in sites where *R. pseudoacacia* is dominant (Peloquin & Hiebert, 1999; Rice *et al.*, 2004; Benesperi *et al.*, 2012; Kou *et al.*, 2016) or a lack of response (Akatov *et al.*, 2012; Sitzia *et al.*, 2012; Masaka *et al.*, 2013; Von Holle *et al.*, 2013). Our results support the latter case as we found no change in plant species richness or diversity in *R. pseudoacacia* plots compared to *Quercus* sp. plots. Contrary to other variables studied here, in this case there was no difference between broad- and regional-scales. Invasion time-scale (i.e. length of invasion) could also play a significant role in explaining this pattern, or lack thereof, as a few studies have demonstrated the delayed impacts *R. pseudoacacia* (Wang *et al.*, 2012; Staska *et al.*, 2014) both on soil nitrate content and plant communities. In our case, most *R. pseudoacacia* belonged to the "middle" class *sensu Staska* with more limited effects compared to more mature plots. Interestingly, we actually found a positive effect of *R. pseudoacacia* on understory plant diversity when mixed with controls (Figure 19e) with diversity following quadratic polynomial function in relation to *R. pseudoacacia* cover (Figure 19f). It is hard to distinguish between a simple response of plant diversity to a higher tree species richness (Mölder *et al.*, 2008; Vockenhuber *et al.*, 2011) and a idiosyncratic response to *R. pseudoacacia* when co-occurring *Quercus* species.

### *4.3. Very limited response of the soil mesofauna*

We tentatively hypothesized, based on the literature, that soil fauna abundance could be negatively affected by replacement of native tree species by *R. pseudoacacia*. Our results did not support this hypothesis as we found no effect of *R. pseudoacacia* cover on the soil fauna. Studies that have focused on the soil macrofauna as a whole (Brygadyrenko, 2015; Buchholz *et al.*, 2015), only soil arthropods (Degomez & Wagner, 2001) or saproxylic beetles (Della Rocca *et al.*, 2016). Among them, most found no significant changes species richness or diversity (Brygadyrenko, 2015; Buchholz *et al.*, 2015; Della Rocca *et al.*, 2016) yet decreased abundance has been found in some cases, for some trophic or taxonomic groups (Degomez & Wagner, 2001; Brygadyrenko, 2015; Buchholz *et al.*, 2015). We chose to focus on soil microarthropods as, with the exception of the work done by Bushcholz, which only considered collembola and not acari, this group of organism has received comparatively lower attention. Another laboratory study focused on *R. pseudoacacia* leaf litter degradation found similar numbers of soil microathropods after incubation in both native and exotic litter despite higher litter quality (Gergócs & Hufnagel, 2016) suggesting that, despite alterations of soil and litter properties, repercussions on the soil fauna may not be drastic at least at low-taxonomic resolutions.

We found almost no support for the hypothesis of decreased soil fauna abundance under *R. pseudoacacia*, which was only found in Catalonia and only for euedaphic collembola (Figure 20). Interestingly this is also the only region where fungal biomass was found to decrease under *R. pseudoacacia*. As most collembola are considered generalist fungivores there may be a link between the two. The overall lack of response matches what was previously found for epiedaphic & hemiedaphic collembola where abundance wasn't affected and actually tended to increase (Buchholz *et al.*, 2015). We actually found this pattern in Normandy where hemiedaphic collembola increased in abundance. Predators were generally the most impacted trophic group within the macrofauna in the literature, mostly through changes in micro-habitat (Degomez & Wagner, 2001; Buchholz *et al.*, 2015). Gamasid acari, as a group, include a large proportion of predators yet remained unaffected in all cases despite changes in organic layer depth (Figure 17, Figure 18), and thus habitat structure, for epigeous soil organisms.

## 5. Conclusion

Our study was able to confirm previous findings, such as increased soil nitrate content and decreased organic layer persistence, and found for the response of native ecosystems to replacement by *R. pseudoacacia* and provide additional insight. By considering multiple sites across a latitudinal gradient, we confirmed that drastic local impacts in a particular area may not me transposable at a larger scale. In some cases, we actually found inverse response patterns depending on region such as with soil fauna abundances. We found no support for the previous findings of decreased plant species richness and diversity or changes in microbial communities. We also found little support for repercussions on the soil fauna, at least with abundances at low taxonomic resolutions. Overall, our findings highlight the need for large-scale studies in order to properly apprehend the impacts of exotic species across their introduced ranges.

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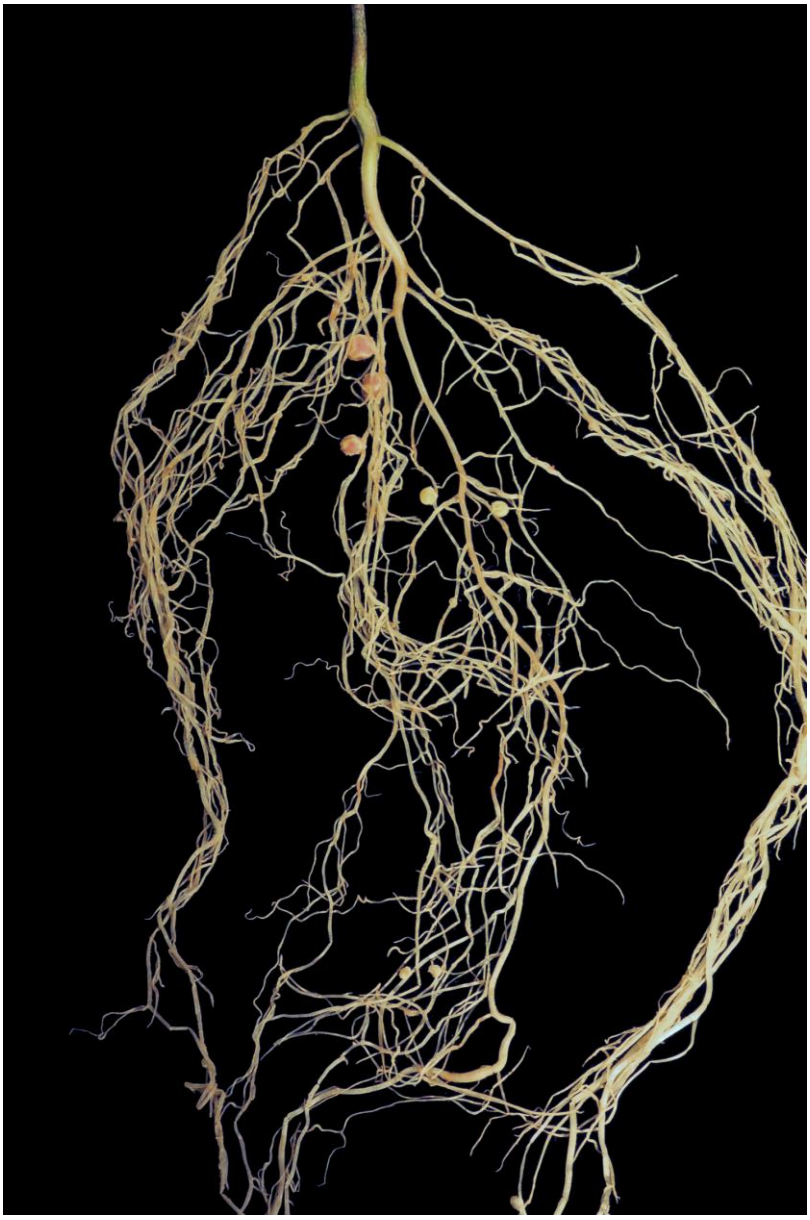
# Chapitre 3 – La réponse fonctionnelle de forêts tempérées au remplacement par une arbre fixateur d'azote, le Robinier faux-acacia (*Robinia pseudoacacia*), est modulée par l'identité de l'espèce native utilisée comme référence



**Nodules racinaires d'un jeune Robinier faux-acacia (*Robinia pseudoacacia*)**

# The functional response of temperate forests to replacement by an exotic nitrogen-fixing tree is modulated by native tree species identity

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## Abstract

Exotic alien species, such as black locust (*Robinia pseudoacacia*; Fabaceae), are a source of increasing concern among anthropogenic global changes due to their propensity to become invasive and their frequent negative environmental effects on native plant communities, nutrient cycling and arthropod communities. Trait differences between exotic and native tree species are thought to be the main drivers of these changes yet traits also differ between native tree species. We aimed to see how relative changes following replacement of native species by *R. pseudoacacia* is dependent on the identity, and traits, of the native species replaced. We sampled native vegetation, soil, soil microorganisms, soil fauna and habitat structure in pure *R. pseudoacacia* plots, pure native plots (either *Quercus petraea* or *Castanea sativa*) and mixed plots within six forests in northwestern France. We observed differences in physico-chemical properties (most notably those related to nitrogen cycling) as well as changes within the soil fauna community. In most cases response differed depending on the considered control with more drastic changes under *R. pseudoacacia* when compared to *Q. petraea* rather than *C. sativa*. *Q. petraea* was the native species with the highest trait difference with *R. pseudoacacia* (notably leaf nitrogen content, specific leaf area and leaf dry matter content) while *C. sativa* had intermediate trait-values. In conclusion, tudying the exotic N-fixing black locust plots in France we observed significantly altered soil functioning, particularly in relation to nitrogen cycling, as well as changes soil fauna communities. These effects were highly species-specific and dependent on the considered native control species. *Q. petraea,* the native control with the most different traits, exhibited the strongest differences with *R. pseudoacacia.*

*Keywords:* ecosystem functioning; soil properties; soil fauna; black locust; Robinia pseudoacacia; invasive trees; plant communities; biological invasions

## 1. Introduction

Introduction of exotic species have received a lot of attention in the past decades due to their frequent escape from plantations or captivity (Vítková *et al.*, 2017) after which they frequently become invasive. Through replacement of native species, change in habitat structure or alteration of ecosystem functioning they can have drastic economic and ecological impact (Vilà *et al.*, 2011; Pyšek *et al.*, 2012) with the rate of these changes expected to increase in the future (Sax & Gaines, 2008). These impacts may result from both direct effects (e.g. allelopathy or competition with natives; Callaway and Ridenour, 2004) or indirectly through changes in the environment (Pyšek *et al.*, 2012). Despite progresses in generalizing the impacts of both exotic and invasive species there remains considerable uncertainty regarding the mechanisms underlying these changes (Schirmel *et al.*, 2016).

Successful introduction of exotic species, and particularly woody trees, is typically related to their ability to opportunistically capture resources (e.g. high relative growth rate and high specific leaf area), which seem to be related to their capacity to translate from exotic to invasive (Shea & Chesson, 2002). Overall differences in performance traits, competitive ability (e.g. allelopathy) or life-history traits have also been demonstrated in many cases between exotic and native species (Callaway & Ridenour, 2004; Van Kleunen *et al.*, 2010b; Castro-Diez *et al.*, 2014). While trait differences are useful in determining invasive potential for an exotic species it does not necessarily relate to the impact said species will exert on native species and ecosystems, and this aspect has been less extensively studied (Pyšek *et al.*, 2012) despite rather conclusive analysis for some ecosystem variables (e.g. carbon pools; Martin *et al.*, 2017). Nevertheless, considerable progress was made on the subject with, for instance, plant woodiness and nitrogen-fixation capability being linked to greater impact of invasive species on carbon and nitrogen cycles (Liao *et al.*, 2008b).

Black locust (*Robinia pseudoacacia* L.) is an exotic, sometime invasive, tree native to south-eastern North America and introduced in Europe in the 16$^{th}$ century (Li *et al.*, 2014) and is one of the most widely planted tree in the world (Keresztesi, 1988). It is a medium-sized hardwood deciduous tree belonging to the subfamily Fabaceae capable of nitrogen-fixation through symbiotic association with rhizobia within root nodules (Wei *et al.*, 2009). In addition to this particular ability, *R. pseudoacacia* tends to exhibit difference in traits related to competitive ability compared to native counterparts (Grotkopp & Rejmánek, 2007). As changes in traits of plant communities are known to drastically alter ecosystem processes and belowground community structure (Vilà *et al.*, 2011; Pyšek *et al.*, 2012; Abgrall *et al.*, 2017), replacement of native tree species by *R. pseudoacacia* could be expected to have drastic effects. If differences in traits are the main drivers of differentiated ecosystem functioning between areas dominated by exotic species and natives (Martin *et al.*, 2017) then trait

differences between native species could be expected to result in dissimilar effects of exotic and/or invasive species depending on the considered native control.

We present the first detailed environmental and multitrophic analysis of the impact of *R. pseudoacacia* introduction in forest ecosystems. As a result of the differences in traits between *R. pseudoacacia* and native species we hypothesized important changes in ecosystem functioning, and native communities, under black locust and tested the following hypotheses: (i) forest ecosystems under the exotic tree Robinia pseudoacacia exhibit altered properties and processes compared to ecosystem under native tree species; (ii) as native species also show variations in functional traits relative responses of ecosystems to exotic trees will be influenced by both the traits of the exotic tree and the traits of the considered native control; (iii) understory vegetation and the soil fauna communities, both taxonomically and functionally, will differ between native and exotic plots due to differences in tree species traits and impacted environmental variables.

*Table 5: Summary of the study sites and plot structure. DBH: Diameter at breast hight. Pure:* Robinia *only; Control: native tree; Mixed:* Robinia *and control.*

| Site | Latitude | Longitude | Elev. (m) | Dominant native tree | Humus forms | Mean *Robinia* canopy cover (%) | | | Mean total *Robinia* basal area ($m^2$) | | | Mean *Robinia* DBH (cm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Pure | Mixed | Control | Pure | Mixed | Control | Pure | Mixed | Control |
| Authouillet | 49°6'27.37"N | 1°17'12.95"E | 108 | *Castanea sativa* | Oligomull | 83.7 ± 1.5 | 48.3 ± 4.1 | 1.1 ± 0.1 | 0.92 ± 0.16 | 0.24 ± 0.12 | 0.008 ± 0.003 | 10.6 ± 5.3 | 8.6 ± 5.7 | 2.5 ± 1.4 |
| Préaux | 49°29'37.46"N | 1°12'3.11"E | 149 | | Mesomull | 72.1 ± 10.1 | 46.8 ± 5.6 | / | 1.12 ± 0.36 | 0.68 ± 0.20 | / | 9.7 ± 2.8 | 11.6 ± 3.9 | / |
| Vaunoise | 48°21'23.44"N | 0°29'26.88"E | 141 | | Oligomull | 76.8 ± 6.1 | 45.2 ± 9.1 | 0.3 ± 0.6 | 1.24 ± 0.32 | 0.72 ± 0.08 | / | 7.3 ± 3.3 | 17.9 ± 3.4 | / |
| Autheuil | 49°6'41.40"N | 1°17'18.93"E | 83 | *Quercus petraea* | Mesomull | 72.2 ± 6.7 | 38.7 ± 8.1 | / | 1.00 ± 0.31 | 0.32 ± 0.07 | / | 11.7 ± 5.2 | 7.2 ± 3.6 | / |
| Mélarbière | 48°21'23.24"N | 0°30'1.22"E | 177 | | Mesomull | 74.2 ± 17.2 | 39.1 ± 6.0 | / | 0.96 ± 0.28 | 0.40 ± 0.12 | / | 10.6 ± 3.3 | 9.9 ± 2.7 | / |
| Pouvrai | 48°16'32.17"N | 0°31'28.53"E | 145 | | Oligomull | 81.9 ± 14.0 | 45.9 ± 13.1 | / | 1.80 ± 0.52 | 0.64 ± 0.24 | / | 12.6 ± 4.2 | 10.0 ± 4.4 | / |

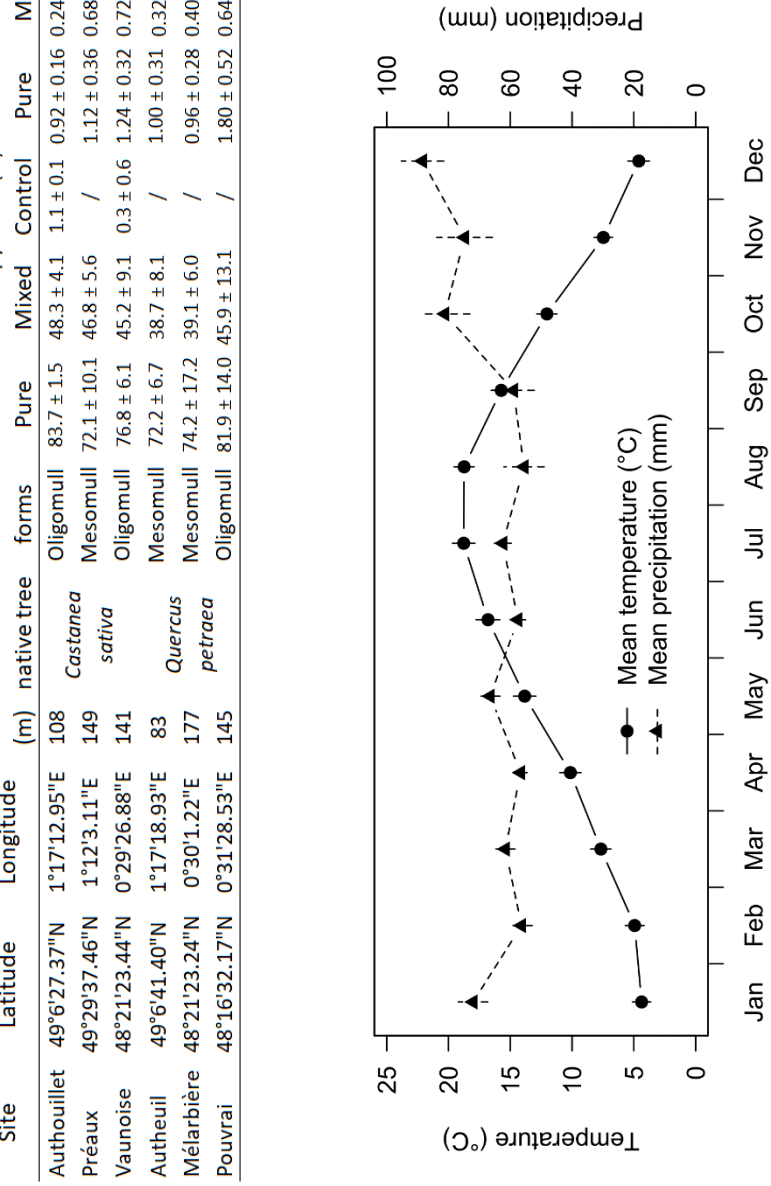


*Figure 21: Mean monthly temperature and precipitation averaged (with standard deviation) from the meteorological stations of Bellême (48°22'38" N; 0°33'41" E), Evreux (49°01'37" N, 1°09'05" E) and Rouen (49° 26' 36" N, 1° 06' 00" E). Data from Météo France (https://donneespubliques.meteofrance.fr/)*

## 2. Material & Methods

### *2.1. Study plots*

The study was carried out within multiple (6) temperate forest sites in Normandy, Northern France in which black locusts (*Robinia pseudoacacia* L., henceforth *Robinia*) are either dominant or mixed with native species (see Table 5 for coordinates and elevation data). In this area, the climate is temperate and oceanic (Cfb in the Köppen classification; see Figure 21 for precipitation and temperature data with seasonal variability). The dominant native tree species are, for the first three forest sites, sweet chestnut (*Castanea sativa* Mill., henceforth *Castanea*) and, for the other three, sessile oak (*Quercus petraeae* (Matt.) Liebl, henceforth *Quercus*) with occasional presence of a small number of other tree species. Humus forms ranged from mesomull to oligomull between sites (Zanella *et al.*, 2011) while being homogeneous within sites.

For each site we chose 3 plots: an exotic-dominated experimental plot (with *Robinia* dominant), a native-dominated control plot (either *Quercus* or *Castanea*) and a mixed plot where *Robinia* occurs together with either *Quercus* or *Castanea* in similar density. We measured circumference at breast height (CBH, 1.3 m) for the three species and then calculated basal area (BA) and diameter at breast height (DBH) from that circumference ($BA = \pi \times [ CBH / ( 2 \times \pi ) ]^2$ and $DBH = CBH / \pi$). We also evaluated canopy cover visually from ground level in order to verify the validity of the choice of these plots (Table 5). *Robinia* canopy cover averaged 76.8 ± 4.9 % and 44.0 ± 4.1 % in exotic-dominated and mixed plots, respectively, while basal area averaged 1.2 ± 0.3 m² and 0.5 ± 0.2 m² within a 314.2 m² area around each sampling point (Table 5).

On each site out of the six we took three samples for each modality (*Robinia*, mixed or control) for a total of 9 samples per site. With two native controls and three sites per species we had a total of 54 sampling point: 2 native control species (*Quercus* or *Castanea*) × 3 replicate sites per species (separate forest areas) × 3 modalities per site (*Robinia*, mixed or control) × 3 pseudoreplicate sampling areas.

### *2.2. Tree species traits*

We used public data from the TRY Plant Trait Database (Kattge *et al.*, 2011) to characterise the three tree species considered in this study. We collected data on maximum height (as mean height is biased by different age classes), specific leaf area, leaf dry matter content (both part of the leaf economic spectrum of plant species and influencing leaf litter quality), nitrogen-fixation capacity (the ability to form root nodules with Rhizobia), type of mycorrhization (particularly the capacity to form symbiosis with arbuscular mycorrhizae), as well as leaf carbon (C) content, leaf nitrogen (N) content,

leaf phosphorus (P) content (all three being linked to resource allocation preference and result in changes in leaf litter quality).

### ***2.3. Soil physico-chemical and microbiological variables***

Soils were sampled for soil physico-chemical, microbiological properties and processes as well as soil fauna and soil microarthropods in late May and early June 2016. A 25 × 25 × 25 cm soil monolith was removed for soil macrofauna sampling (see the section below) and we used that soil profile to measure organic layer depth (OL, OF and OH) and identify humus form (Tab. 1).

We evaluated bulk density using the cores method (Hao *et al.*, 2008). Soil samples collected in 100 $cm^3$ stainless steel cylinders of approximately 5 cm height. Each cylinder was then closed at both ends with plastic caps and transported to the laboratory. These samples were dried at 105 °C for 24 h in an oven. The dry mass of the soil divided by the cylinder volume, after removing the mass and volume of coarse elements (i.e. rocks and root debris) from the calculation, gave the bulk density in $g.cm^3$. We measured pH using 10 g soil samples diluted in 25 ml of ultrapure water (i.e. Milli-Q) or a 1:2.5 mass to volume ratio (Hendershot *et al.*, 1993). Measurements were carried out after 30 min of intermittent stirring and 1 h of decantation. Relative humidity was calculated by weighting the same soil sample before and after 24h of oven drying at 105 °C. Soil water holding capacity was calculated by saturating a soil sample in water for 2h before letting gravitic water run-off and weighting the sample prior and after oven drying at 105°C for 24h. Total carbon and nitrogen were measured using precisely weighted 50 ± 0.05 mg dry soil samples in a ThermoFisher Flash Analyzer 2000.

Potential carbon mineralization, as a surrogate for *in situ* soil respiration, was measured using the closed chamber incubation method with alkali $CO_2$ traps (Hopkins, 2007). 15 g of fresh soil was added to each chamber. Prior to incubation, the moisture content of the soil sample was adjusted to 60% of water holding capacity by adding the corresponding volume of deionized water. 20 ml of 0.5 M sodium hydroxide (NaOH) solution of known conductivity and contained in a scintillation flask was added to each chamber in order to capture $CO_2$. Every 7 days the NaOH solution conductivity was measured and the solution replaced. Incubation itself lasted 14 days at 28°C thus only accounting for the readily mineralizable fraction of the soil organic matter.

Microbial biomass was estimated using the chloroform ($CH_3Cl$) fumigation-extraction method (Voroney *et al.*, 2008). Two 20 g samples of fresh soil were extracted, either with or without a 24h $CH_3Cl$ fumigation in a vacuum chamber, in 100 ml of a 0.2 M potassium sulphate ($K_2SO_4$) solution. Total organic carbon was measured in both samples using the NPOC method in a Shimadzu TOC-L Total Organic Carbon Analyzer. Fungal biomass was estimated using ergosterol content, a sterol found

within fungi and protozoa, and the method proposed by Gong, Guan & Witter (2001). Four grams of fresh soil were used to measure ergosterol content using high-performance liquid chromatography (ThermoFisher Scientific UltiMate 3000 UHPLC) and a commercially available ergosterol solution.

Soil mineral nitrogen content was evaluated by measuring nitrate ($NO_3^-$) and ammonium ($NH_4^+$) content following extraction of 20g of soil in 100 ml of 0.2 M NaOH and using a ThermoFisher Gallery Automatic Sequential Analyzer. Potentially mineralizable nitrogen was evaluated by coupling the method proposed by Curtin and Campbell (2008) with the aforementioned closed chamber incubation method. In addition to the initial measurement of $NO_3^-$ and $NH_4^+$ content we used the methodology after 14 days of incubation using the incubated soil sample.

Litter decomposition rate (LDR) was quantified using the litter bag method with exogenous litter in order to avoid home field advantage effect (Ayres *et al.*, 2009). We used 3.0 ± 0.10 g of dry European beech (*Fagus sylvatica* L.) and field maple (*Acer campestre* L.) litter in 20 × 15 cm bags with a mesh size of 1 cm. This large mesh size was used in order to allow access to the litter by the whole soil fauna. 3 litter bags were used for each species at each sampling point, for a total of 324 litter bags, and one was collected after 3, 6 and 9 months between December 2016 and September 2017. LDR was measured by calculating the relative mass loss by a unit of time.

### ***2.4. Understory vegetation***

Understory vegetation was sampled in late June and early July 2016. We sampled vegetation cover in a 5 × 5 m area centred around the soil sampling point using the Braun-Blanquet cover-abundance scale. We found 47 different species of forbs and flowering plants in the 6 sites (Appendice C). In addition to cover-abundance data all vegetation within a 1 × 1 m area centred around the soil sampling point was collected in order to measure plant biomass. These samples were then dried and weighted in order to obtain the biomass for each species.

At each sampling point species representing less than 5 % of total biomass were removed prior to analysis as soil processes are frequently related more to dominant traits rather than functional diversity itself, especially in low productivity sites such as ours (e.g. nitrification: Laughlin, 2011). Traits within the leaf economic spectrum were either directly measured on individuals collected in the field or obtained from the TRY Plant Trait Database (Kattge *et al.*, 2011). Measured traits were leaf area ($mm^2$), leaf fresh mass (g), leaf dry mass (g) from which we computed leaf dry matter content ($mg.g^{-1}$) and specific leaf area ($mm^2.mg^{-1}$). We also measured leaf nitrogen and carbon content ($mg.g^{-1}$) from which we computed the carbon-to-nitrogen ratio using a ThermoFisher Flash Analyzer 2000. We obtained data on maximum plant height (m) and seed dry mass (g) from the TRY database.

### *2.5. Soil microfauna & microarthropods*

At the end of the experiment, several biotic and abiotic variables were assessed. Approximately 100g of fresh soil was used for microarthropod extraction in a Berlese-Tullgren funnel (Macfadyen, 1961). Samples were weighted and placed within sieves (stitch: 1 mm, diameter: 80 mm, height: 50 mm) above a plastic funnel. Extraction, under a heat source, lasted for a week with individuals collected in 70% ethanol. This extraction method is dependent on the limited tolerance of these animals to desiccation and will therefore only extract active individuals. There is therefore no differentiation between individuals that were inactivated, killed or otherwise incapacitated. One hundred grams of fresh soil was used for nematode extraction in a Baermann funnel (McSorley & Walter, 1991). Dampened samples were placed in a porous paper (10-15 µm stitch) supported by a 2 mm sieve and placed above a water-filled and sealed funnel for 48h. This method has a limited efficiency in isolating slow moving and nematodes and will not isolate inactive individuals (Van Bezooijen, 2006) and thus is not exhaustive but allow simultaneous processing of a large number of samples.

Microarthropods samples were separated into Acari and Collembola under a stereo binocular microscope. Collembola individuals were mounted in lactic acid on microscope slides for identification to the species level (Potapov, 2001; Thibaud, 2004; Hopkin, 2007) with a phase-contrast optical microscope. Acari were identified to the order or suborder level: Mesostigmata (Gamasida), Cryptostigmata (Oribatida) and Prostigmata (Actinedida) (Coineau & Cleva, 1997). The cohort Astigmatina (previously the suborder Astigmata) were included in the suborder Oribatida (Wang & Fan, 2010). After Baermann funnel extraction, nematodes were counted while active under a stereo binocular microscope. Following decantation nematodes were fixed using a 4% formaldehyde solution and mounted on microscope slides. Individuals were attributed to trophic groups (herbivores, bacterivores, fungivores and predators/omnivores) based on mouthpart examination under a compound optical microscope.

For collembola, we used trait data from the COLTRAIT/BETSI database (http://betsi.cesab.org/; BETSI, 2012; Salmon *et al.*, 2014). Selected traits were representative of dispersion capacity (body shape, body length, furca length), defence mechanisms (presence of scales) and resource management (presence of visual organs, number of lobes of the post-antennal organs). Unordered qualitative variables were split into dummy variables for analyses.

### *2.6. Soil macrofauna*

Soil macrofauna was sampled concurrently with soil microarthropods and the soil microfauna. First, the organic (OL, OF and OH in the rare cases where the latter was present) layers were removed

on a 25 × 25 cm area and placed in a tray where macrofauna was hand-sorted for 15 min. A 25 × 25 × 25 cm soil monolith was then dug out, placed in a tray, and hand-sorted for 30 min. In both cases specimens were placed in 70% ethanol ($C_2H_6O$) for transport and storage. All specimens were identified in the lab with the help of a stereoscopic magnifier. Adult earthworms, millipedes, centipedes, woodlice and snails/slugs were identified to the species level using locally available keys for each group (Brolemann, 1935; Hopkins, 1991; Kerney & Cameron, 1999; Barber, 2008; Sherlock, 2018). Other soil organisms within the soil fauna, such as coleopteran or other insect larvae, were identified to the order level. We used trait data from the BETSI database (http://betsi.cesab.org/; BETSI, 2012). Selected traits were representative of trophic preference (Geophages, Phytophages, Detritivores and Zoophages), dispersal ability (Body length) and preferential habitat (Visual organs).

### ***2.7. Statistical analysis***

We used principal components analysis (PCA) to plot the multivariate trait differences between the exotic and the two native tree species. As data sources differed between traits (due to their different origin within the TRY Plant Trait Database) the "samples" within the sample × trait matrix are not real entities and representing them as such could lead to spurious conclusions. We thus used generated randomized permutations of samples within the trait matrix and used average scores for plotting thus confirming that the results are not due to a stochastic, or deliberate, process. In addition, we confirmed these results independently and quantitatively through analysis of variance (ANOVA) for each considered quantitative trait.

Partial redundancy analysis (pRDA) is an alternative to canonical correlation analysis (CCorA) the enables quantitative evaluation of the relationship between two matrices, **X** and **Y** (Legendre & Legendre, 2012). In CCorA the components of variability from the two matrices are extracted so that correlation between the two are maximised. In pRDA, the components from **X** (i.e. matrix of environmental variables) are extracted so as to be as correlated as possible to **Y** (i.e. matrix of aggregated basal area and canopy cover for the three tree species) using unweighted linear regression and singular value decomposition. This reveals the influence of variables within **Y** on those within **X** in an operation known as "constraining" which, here, shows the response of environmental variables to the presence or dominance of exotic and native tree species. In addition, pRDA enables the removal of the effect of a third matrix, **Z**, from matrix **X** with the residual matrix (**X'**) being submitted to "constraining". This process, called "conditioning" is used here to remove site effects from the data environmental matrix. Both "constraining" and "conditioning" can be quantified thus enabling a rough indication of the components of variance within **X** based on **Y** and **Z** or the explanatory power of both.

For all variables measured in the field, both biotic and abiotic, we calculated the relative differences between treatments and controls by standardizing and normalizing our measured values in relation to control means. We did this by subtracting the average control value to each individual values within *Robinia*, and mixed, modalities and dividing it by the control mean thus providing a relative difference from which we extracted across-site means and standard deviations. We used wilcoxon rank-sum tests to assess the significance of these differences. We either presented the results in a table or using barplots for graphical representation.

We calculated indices to characterise and synthetize community properties for understory plants, Collembola and several groups of soil macrofauna (earthworms, millipedes, centipedes, woodlice and snails/slugs). We used species identification along with their corresponding abundance, or cover for plants, to compute community species richness (S), diversity (Shannon Index; H) and evenness (Pielou Index; J = H/log(S)) within each sampling area. Additionally, we used abundance and trait data to compute functional diversity indices (Functional richness, evenness and divergence; Villéger *et al.*, 2008) and community-weighted average trait values within each sampling area.

## 3. Results

### 3.1. Trait differences between tree species

Results show important differences in traits between the exotic and native trees considered here (Figure 22). *Robinia* is characterized by its nitrogen fixation ability, which is lacking in both *Quercus* and *Castanea* while differences in preferential mycorrhizas also discriminates between the three species. There are important differences between the three species for leaf nitrogen content ($F = 26.95$, $R^2 = 0.64$, $p < 0.00001$) and maximum height ($F = 46.13$, $R^2 = 0.76$, $p < 0.00001$). There are only differences between *Robinia* and *Quercus* for leaf carbon content ($F = 4.871$, $R^2 = 0.21$, $p < 0.05$) and leaf dry matter content ($F = 7.076$, $R^2 = 0.30$, $p < 0.01$) with no differences in traits between *Robinia* and *Castanea*. There are no differences in leaf potassium content ($F = 1.688$, $R^2 = 0.05$, $p = 0.20$) and specific leaf area ($F = 3.289$, $R^2 = 0.14$, $p = 0.0527$) despite a tendency for *Robinia* to have higher values of SLA compared to both other species.

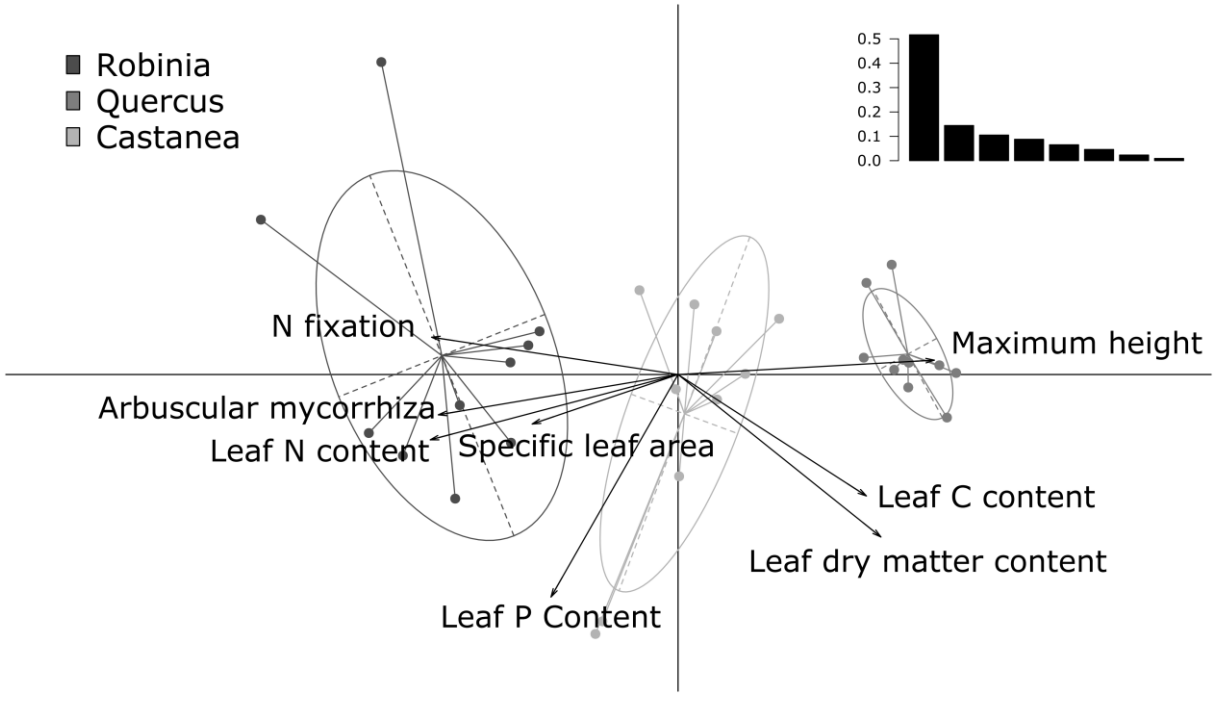


*Figure 22: Principal components analysis (PCA) biplot of trait differences between the considered exotic tree species (Robinia pseudoacacia) and the two native tree species (Quercus petraea & Castanea sativa). Data was measured from samples taken in the field (Leaf dry matter/carbon/nitrogen content and specific leaf area) while others were obtained from the TRY Plant Trait Database (www.try-db.org).*

### *3.2. Differences in response of soil variables*

Partial redundancy analysis (pRDA) of environmental variables and processes conditioned by site effect and constrained by tree species cover and basal area enabled a rough extraction of components of variance. This showed that site effect accounted for 25.2%, and tree species (i.e. both exotic and nativs) effect for 8.5%, of the variance in the dataset with 66.3 % unconstrained, or unexplained, variance (Figure 23). The first pRDA axis shows a distinction between plots dominated by *Robinia* and plots dominated by native tree species. Ammonium ($NH_4^+$) content, bulk density and potential ammonification were positively correlated to native control dominance while potential respiration, nitrate ($NO_3^-$) content, soil relative humidity and water holding capacity were positively correlated to *Robinia* dominance. The second pRDA axis, accounting for half the variance of the first axis, shows a distinction between *Quercus* and the two other species. In this case organic layer depth, canopy cover and fungal biomass were positively correlated to *Quercus* dominance while nitrate ($NO_3^-$) content and potential nitrification were positively correlated to *Castanea* or, more strongly, *Robinia* dominance.

*Table 6: Relative differences for soil and floral variables between native control plots and* R. pseudoacacia *plots*

| Modality | | Mixed *Robinia pseudoacacia* | | | | Pure *Robinia pseudoacacia* | | | |
|---|---|---|---|---|---|---|---|---|---|
| Native control | | *Castanea sativa* | | *Quercus petraea* | | *Castanea sativa* | | *Quercus petraea* | |
| ***Soil physicochemistry, microbiology and processes*** | Bulk density | **-14.4 ± 5.7** | * | 8.7 ± 12.3 | | **-34.4 ± 7.7** | ** | -4.1 ± 7.3 | |
| | Canopy cover | **28.1 ± 8.9** | * | -27.4 ± 12.6 | | 38.3 ± 21.7 | | **-16.7 ± 6.4** | * |
| | Fungal biomass (Ergosterol) | 10.0 ± 14.6 | | 28.2 ± 22.3 | | -17.6 ± 28.0 | | 8.1 ± 23.7 | |
| | Microbial biomass (C) | 5.4 ± 14.5 | | 3.5 ± 11.4 | | 0.8 ± 16.3 | | -2.7 ± 12.2 | |
| | Organic layer depth | 28.9 ± 15.3 | | 29.4 ± 19.4 | | 25.9 ± 12.3 | | -8.9 ± 22.9 | |
| | pH | 1.6 ± 6.3 | | 1.4 ± 7.3 | | -3.9 ± 6.1 | | -4.1 ± 7.4 | |
| | Relative humidity | 3.7 ± 5.4 | | 8.6 ± 5.7 | | 5.0 ± 5.4 | | **20.8 ± 6.2** | ** |
| | Water holding capacity | 11.0 ± 5.8 | | **16.9 ± 6.0** | * | 58.9 ± 45.1 | | 9.0 ± 14.0 | |
| ***Understory vegetation*** | Biomass | 29.7 ± 21.1 | | 47.0 ± 51.8 | | 32.2 ± 31.4 | | 86.9 ± 51.1 | |
| | Species richness | 31.1 ± 26.1 | | 5.3 ± 6.9 | | 7.8 ± 21.0 | | 6.6 ± 16.4 | |
| | Shannon's diversity | 67.0 ± 46.1 | | 5.1 ± 11.1 | | 51.5 ± 41.6 | | 21.6 ± 14.6 | |
| | Pielou's evenness | 23.0 ± 30.1 | | 0.0 ± 10.2 | | 27.5 ± 34.0 | | 12.5 ± 6.0 | |
| | Functional divergence | 45.9 ± 23.9 | | -13.9 ± 7.2 | | 48.1 ± 32.0 | | -4.5 ± 7.9 | |
| | Functional evenness | 18.3 ± 34.9 | | 4.8 ± 14.4 | | 24.8 ± 28.3 | | 7.3 ± 13.3 | |
| | Functional richness | 140.0 ± 121.7 | | -11.0 ± 15.9 | | 145.5 ± 124.0 | | 19.6 ± 24.8 | |
| | Leaf dry matter content | -8.8 ± 4.5 | | -11.6 ± 6.9 | | -18.9 ± 8.7 | | **-17.9 ± 7.0** | * |
| | Leaf nitrogen content | -1.4 ± 2.3 | | 7.3 ± 10.3 | | 2.5 ± 1.4 | | 15.4 ± 8.7 | |
| | Maximum height | -2.9 ± 19.5 | | 124.8 ± 101.2 | | **-38.0 ± 9.1** | ** | 221.0 ± 154.8 | |
| | Seed dry mass | 47.7 ± 72.7 | | 1.2 ± 26.2 | | **-49.4 ± 9.2** | *** | 263.8 ± 139.1 | |
| | Specific leaf area | 3.7 ± 5.5 | | 18.1 ± 14.6 | | 2.6 ± 4.6 | | **34.0 ± 11.8** | * |

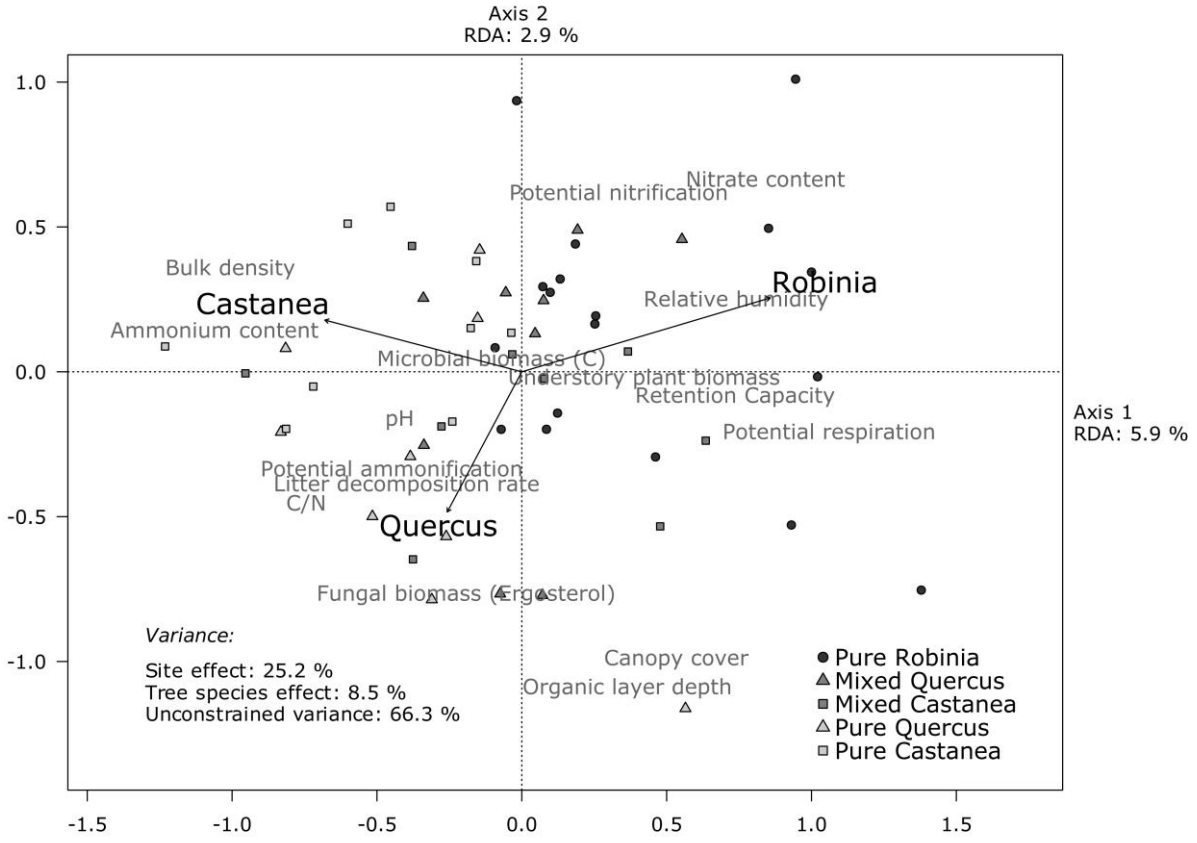


*Figure 23: Redundancy analysis (RDA) biplot of the tree species cover and ecosystem properties & processes (after removal of site effect). Black arrows and text show the result of constraining the RDA based on tree species (basal area and cover) of both the exotic tree (R. pseudoacacia) and the two native controls (Q. petraea & C. sativa). Light grey text shows various environmental properties and processes after removal of site effect (conditioning) and maximisation of correlations with the tree species cover matrix (constraining). Black dots are individual sites after ordination by principal components analysis (PCA) following conditioning and constraining.*

### ***3.3. Nitrogen and organic matter cycling***

Soil ammonium ($NH_4^+$) shows distinct responses to *Robinia* depending on the considered native control with a strongly negative response when compared to *Castanea* in pure plots (-57 ± 9 %, $p < 0.001$, Figure 24a) but no change compared to *Quercus* (-10 ± 38 %, n.s.). Conversely the opposite is true in mixed plots with a negative response compared to *Quercus* control (-41 ± 17 %, $p < 0.05$) and no response compared to *Castanea* control. Changes in potential ammonification are all negative responses to *Robinia* both in pure and mixed stands compared to *Quercus* controls (-75 ± 8 %, $p < 0.001$ and -58 ± 8 %, $p < 0.001$, respectively, Figure 24b) and in pure *Robinia* stands only when compared to *Castanea* (-66 ± 26 %, $p < 0.05$) with no significant response in mixed *Castanea* plots. The effect of *Robinia* on nitrate ($NO_3^-$) content appears to be inverse, and positive, with an increase in both mixed and pure plots when compared to *Quercus* dominated control plots (+124 ± 30 %, $p < 0.01$ and +191 ± 81 % , $p < 0.05$, respectively, Figure 24d) and no significant response compared to *Castanea* plots.

Potential nitrification was not significantly affected in *Robinia* plots although there was a negative trend in both mixed and pure plots with a *Quercus* control (-550 ± 391 % and -148 ± 233 %, respectively, Figure 24e) despite a strong variability in the results. Soil carbon-to-nitrogen ratio decreased significantly in pure *Robinia* plots compared to the *Quercus* control (-13 ± 3 %, $p < 0.01$, Figure 24c) resulting from an increase in soil total nitrogen content (+136 ± 32 %, $p < 0.01$, Figure 24f) while there were no changes in mixed plots or in pure *Robinia* plots when compared to *Castanea* plots.

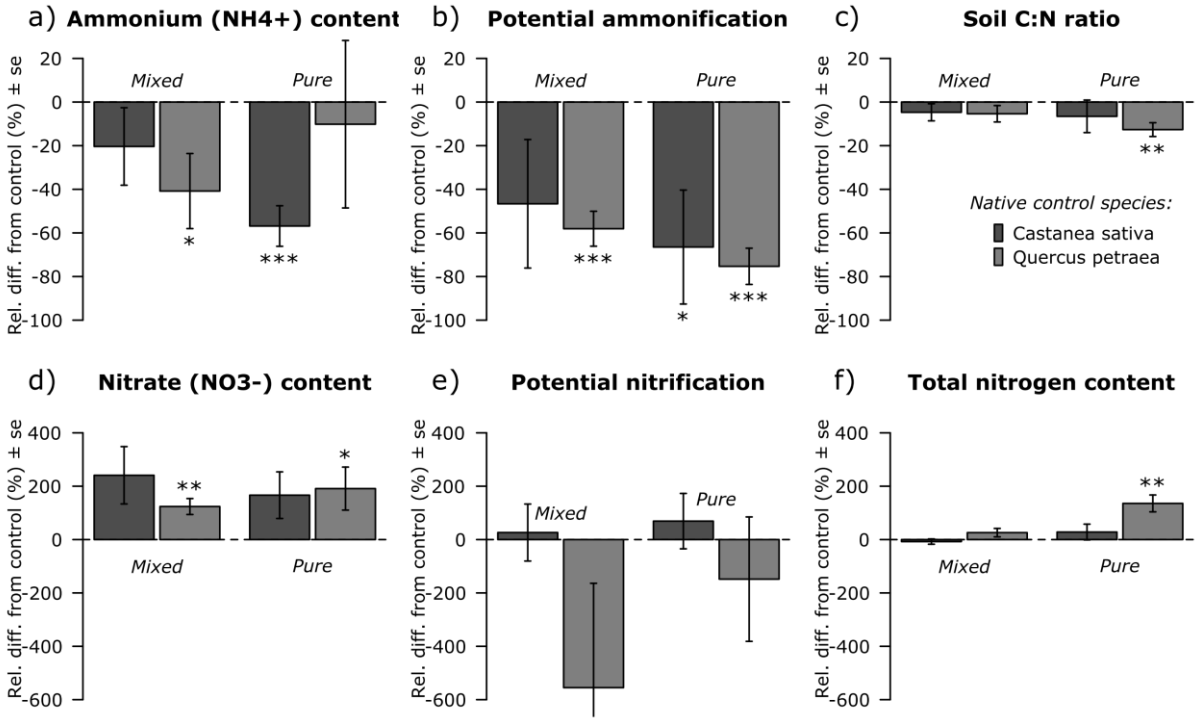


*Figure 24: Relative differences between mixed and pure Robinia pseudoacacia plots and native control plots (Castanea sativa or Quercus petraea) for variables related to nitrogen cycling. Symbols indicate levels of significativity of repeated statistical testing of differences between calculated values and null generated controls.*

Both carbon mineralization (potential respiration), measured in controlled condition, and litter decomposition rate, measured in the field, increased significantly in pure *Robinia* stands compared to *Castanea* stands (+48 ± 7 %, $p < 0.05$ and +141 ± 51 %, $p < 0.05$, respectively; Figure 25), but not compared to pure *Quercus* control plots. There were no differences between pure control plots and mixed *Robinia* plots.

As suggested by Figure 3, statistical analysis of relative differences between *Robinia* and controls shows some strong response to *Robinia* presence (Figure 24). There are also differences in response between the controls themselves (Figure 24). Soil bulk density (mixed and pure, compared to *Castanea* plots), canopy cover (in mixed *Castanea* and pure *Robinia* compared to *Quercus*) was well as relative humidity (pure *Robinia* with *Quercus* control) water holding capacity (in mixed *Quercus* plots) were negatively or positively affected by *Robinia* presence.

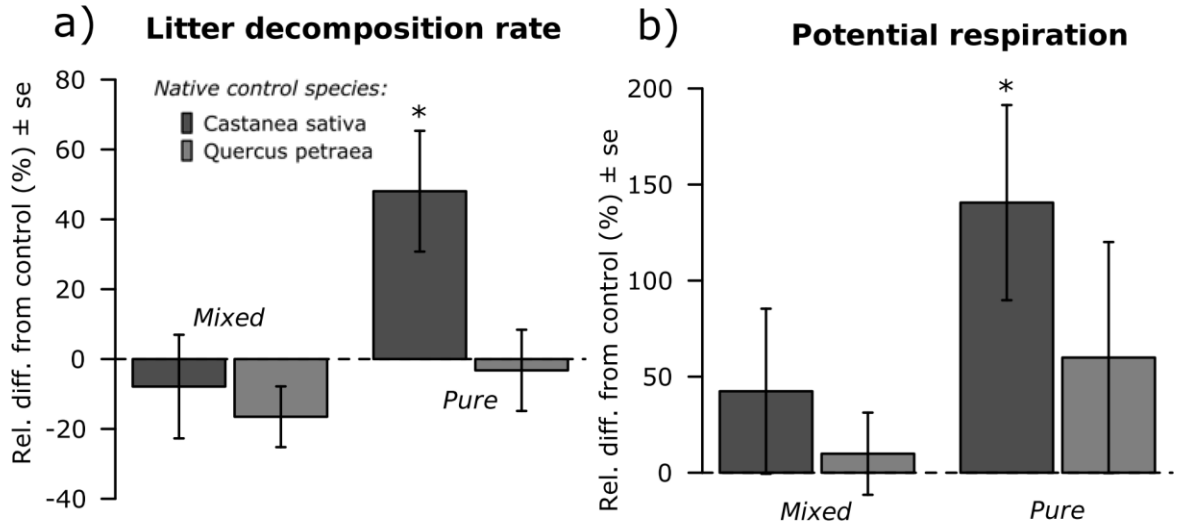


*Figure 25: Relative differences between mixed and pure Robinia pseudoacacia plots and native control plots (Castanea sativa or Quercus petraea) for variables related to carbon mineralization. Symbols indicate levels of significativity of repeated statistical testing of differences between calculated values and null generated controls.*

### ***3.4. Understory vegetation and the soil fauna***

Understory vegetation communities appeared largely unaffected both taxonomically and functionally although traits community-weighted means (CWMs) were, to some extent (Table 6). Leaf dry matter content and specific leaf area were negatively and positively affected, respectively, by *Robinia* dominance when compared to a *Quercus* native control. Maximum height and seed dry mass were both negatively affected by *Robinia* dominance compared to a *Castanea* control.

Soil macrofauna species richness (Table 7) was positively affected by *Robinia* dominance (i.e. pure plots) when compared to a *Quercus* control, but not by *Robinia* presence (i.e. mixed plots). Both functional divergence and functional evenness were negatively affected in pure *Robinia* plots compared to the *Castanea* control plots. There was a significant increase in the number of geophages (mostly earthworms) and phytophages (mostly snails and slugs) in mixed and pure *Robinia* plots compared to *Quercus* control plots. The opposite was true for geophages in pure *Robinia* plots, but not mixed plots, compared to *Castanea* control plots. Average body length in the community also decreased in this plots while ratio of individuals with visual organs increased, both being traits in which earthworms differ from the rest of the community. Finally, detritivores were negatively affected in *Robinia* dominated plots with *Quercus* control.

Acari abundance was negatively affected by *Robinia* presence and dominance when compared to *Quercus* control plots while Nematoda abundance remained unaffected in all cases. Collembola abundance was positively affected but only when considering *Castanea* as a control with no effect when considering *Quercus*. Collembola species richness and diversity were negatively affected in pure *Robinia* plots with *Quercus* control yet diversity was positively affected in mixed *Robinia* plots compared to *Castanea* control. Regarding traits community-weighted means only the presence of scales, a trait related to defence and an epigeous lifestyle, was positively affected by *Robinia* presence but only in mixed plots with *Quercus* control.

*Table 7: Relative differences for soil macrofauna et mesofauna between native control plots and R. pseudoacacia plots*

| | **Modality** | **Mixed *Robinia pseudoacacia*** | | **Pure *Robinia pseudoacacia*** | |
|---|---|---|---|---|---|
| | **Native control** | ***Castanea sativa*** | ***Quercus petraea*** | ***Castanea sativa*** | ***Quercus petraea*** |
| ***Soil macrofauna*** | Abundance | -23.2 ± 13.9 | 19.6 ± 23.8 | -22.7 ± 14.6 | 41.6 ± 27.7 |
| | Species richness | -6.6 ± 10.4 | 32.8 ± 22.2 | -21.9 ± 13.0 | **41.0 ± 17.5** * |
| | Shannon's diversity | -3.7 ± 8.3 | 31.0 ± 19.5 | -18.6 ± 13.7 | 33.7 ± 18.5 |
| | Pielou's evenness | -4.4 ± 4.1 | -4.0 ± 6.1 | -1.0 ± 3.1 | -4.0 ± 5.0 |
| | Functional divergence | -12.8 ± 6.6 | -1.3 ± 3.6 | **-18.0 ± 3.6** ** | -10.5 ± 5.5 |
| | Functional evenness | -12.0 ± 13.2 | 2.4 ± 7.6 | **-41.1 ± 7.2** ** | -1.5 ± 5.9 |
| | Functional richness | -31.5 ± 14.0 | 45.2 ± 38.9 | -48.4 ± 28.2 | 35.5 ± 33.1 |
| | Body length | -1.7 ± 6.9 | 38.0 ± 20.9 | **-25.3 ± 9.1** * | 8.1 ± 12.8 |
| | Visual organs | -1.1 ± 11.9 | -13.3 ± 6.4 | **51.8 ± 17.5** * | -1.4 ± 4.8 |
| | Geophages | -30.1 ± 24.7 | **229.0 ± 34.0** * | **-88.1 ± 11.0** *** | **237.0 ± 41.0** * |
| | Phytophages | 16.7 ± 9.3 | **25.0 ± 10.7** * | 11.3 ± 12.1 | **33.4 ± 11.9** * |
| | Detritivores | -22.5 ± 10.9 | -16.8 ± 10.2 | -21.7 ± 14.0 | **-27.0 ± 5.3** *** |
| | Zoophages | 129.9 ± 70.6 | -35.4 ± 17.3 | -43.5 ± 27.9 | -23.5 ± 15.9 |
| ***Soil mesofauna*** | Acari abundance | -7.8 ± 12.4 | **-37.9 ± 11.4** * | 29.2 ± 14.3 | **-38.6 ± 13.2** * |
| | Nematoda abundance | -11.1 ± 11.3 | -6.7 ± 1932.0 | -0.4 ± 40.0 | 27.6 ± 13.8 |
| | Collembola abundance | **49.1 ± 13.0** ** | -27.2 ± 14.5 | **145.9 ± 44.0** * | -3.9 ± 25.0 |
| | Species richness [1] | 25.3 ± 14.4 | -10.0 ± 13.1 | 22.7 ± 21.6 | **-33.2 ± 10.6** * |
| | Shannon's diversity [1] | **16.3 ± 6.8** * | -10.7 ± 9.3 | 9.0 ± 12.0 | **-23.6 ± 8.3** * |
| | Pielou's evenness [1] | -2.9 ± 2.4 | -6.7 ± 5.2 | -7.0 ± 3.4 | -7.3 ± 4.5 |
| | Functional divergence [1] | 3.7 ± 2.2 | 4.7 ± 2.2 | -0.4 ± 3.3 | -1.0 ± 3.3 |
| | Functional evenness [1] | 0.5 ± 2.8 | 3.6 ± 3.3 | 6.0 ± 3.4 | -5.1 ± 3.0 |
| | Functional richness [1] | -18.7 ± 14.5 | 6.7 ± 17.5 | -27.7 ± 17.8 | 2.3 ± 17.1 |
| | Furca length [1] | -2.0 ± 4.5 | 1.0 ± 2.5 | 3.7 ± 3.6 | 3.6 ± 3.0 |
| | Post-antennal organ lobes [1] | -3.7 ± 9.4 | -15.0 ± 8.3 | 5.2 ± 8.0 | -7.8 ± 3.5 |
| | Body length [1] | 16.7 ± 9.5 | 11.8 ± 7.1 | 4.2 ± 5.2 | 0.6 ± 3.3 |
| | Body shape [1] | 1.3 ± 1.2 | -1.6 ± 1.5 | 0.2 ± 1.7 | 0.8 ± 1.2 |
| | Scales presence [1] | -11.2 ± 12.4 | **63.2 ± 16.9** ** | -11.1 ± 8.8 | -11.1 ± 15.9 |
| | Visual organs presence [1] | -5.3 ± 3.1 | 4.8 ± 4.2 | -7.5 ± 4.2 | -3.4 ± 3.5 |

## 4. Discussion

Plots with *Robinia pseudoacacia* exhibit altered properties and processes notably through differences in organic matter mineralization and, particularly, nitrogen cycling. Concomitantly, the soil fauna showed functional changes within communities but was largely unaffected taxonomically. Furthermore, contrary to what is frequently suggested in the literature there was no decrease in native understory plant diversity under *Robinia* although there were some changes in community–level traits. Considering the two native control species separately yielded interesting results with frequently contrasting responses for both abiotic and biotic soil variables under *Robinia* depending on the considered native control. *Robinia* generally had the most drastic effect when compared to *Quercus*, the native species exhibiting the largest trait difference with *Robinia*.

### *4.1. From leaf to litter: differences in traits*

Our results show significant differences between the traits of the exotic tree and its native counterparts, yet the two native species also differed strongly from each other regarding some particular traits (Figure 22). *Robinia* was qualitatively separated from the two native species due to its known ability to fix atmospheric nitrogen through root nodules while the two natives differ in that *Quercus* is primarily ectomycorrhizal (EM) (as is *Robinia*) while *Casteanea* is primarily arbusco-mycorrhizal (AM). Tree species with AM tend to exhibit increased specific root area and favours inorganic phosphorus uptake while EM favours nitrogen uptake (Kubisch *et al.*, 2015), which may explain the lack of EM in *Robinia* as its association with rhizobia provide the same service to the host. Maximum height differences between the three tree species (*Quercus* > *Castanea* > *Robinia*) are probably related to the successional status of each species with *Robinia* being a heliophilous pioneer species in early successions while *Castanea* and *Quercus* are shade-tolerant postpioneers (Rameau *et al.*, 1989).

While annual litterfall was not measured in the field the litterature suggests limited differences between the three species with values ranging from 3.1 to 4.8 $t.ha.yr^{-1}$ with high context-dependant variability (Anderson, 1973; Ranger & Colin-Belgrand, 1996; Lee *et al.*, 2011). *Robinia* has the highest nitrogen content in its leaf (34.9 ± 6.3 $mg.g^{-1}$) compared to *Castanea* and *Quercus* (23.7 ± 6.8 and 16.2 ± 3.3 $mg.g^{-1}$, respectively) while there were no differences in leaf potassium content or specific leaf area. This results in contrasted litter nutritional quality with similar quantity. Moreover, the significantly lower leaf dry matter content of *Robinia* compared to *Quercus* (but not *Castanea*) improves palatability for detritivorous species. Both should, in theory, result in accelerated litter degradation of *Robinia* litter.

There was no change in organic layer depth (Table 6) suggesting that the soil was not sufficiently affected to alter basic functioning and humus form, at least in the considered timeframe since *Robinia* was introduced. There was, however, a twofold increase in litter decomposition rate (LDR) in mixed *Castanea* plots which was matched by a threefold increase in potential respiration (PRE; Figure 25). LDR has been found to increase under *Robinia* in another study also using *Quercus* ssp. as a native control (Lee *et al.*, 2011). Changes of that magnitude should be linked to increased detrital or microbial activity yet both fungal and microbial biomass were unaffected as was the prevalence of detritivores among the soil macrofauna (Table 6, Table 7). Several studies, however, have pointed to a weak link between microbial or ergosterol biomass and microbial activities (Bolton *et al.*, 1993). Among measured variables, only the increase in collembolan abundance (i.e. fragmenters and microbivores) could partially explain increased litter decomposition in the field, yet not potential respiration, measured in the lab where only the microbial component of the detrital food web is present. *Robinia* leaf litter is, in the literature, considered as more readily decomposable due to decreased lignin content (Landgraf *et al.*, 2005) and a lower dry matter content (Figure 22) thus increasing the overall mineralization process. If that was indeed the case LDR would be expected to be increased in all experimental plots, and particularly pure *Robinia* plots while it appears that only mixed *Robinia*-*Castanea* results in an increase in LDR.

### ***4.2. From ammonium to nitrate: nitrogen and carbon cycling***

We expected significant changes in ecosystem properties based on a literature review yet found limited support for these drastic changes in our case. Due to its nitrogen fixation properties there have been numerous studies on nitrogen cycle under *Robinia* and it has been suggested as the main driver of *Robinia* impact on native ecosystems (Terwei *et al.*, 2016).

Our results shows that the presence or dominance of *Robinia* does indeed affect various aspect of the nitrogen cycle. Soil C:N ratio decreased (through a slightly higher total nitrogen content and markedly lower total carbon content) in plots dominated by *Robinia* compared to native *Quercus* plots, but not compared to native *Castanea* (Figure 24). This lack of difference in the case of *Castanea* contrasts with the literature where soil nitrogen content has been found to increase in most cases (Rice *et al.*, 2004; Landgraf *et al.*, 2005; Taniguchi *et al.*, 2009; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2016) but not all (Von Holle *et al.*, 2006). In these studies the control differed wildly with scots pine (*Pinus sylvestris*; Landgraf *et al.*, 2005), white poplar (*Populus alba*; Medina-Villar *et al.*, 2016), mixed pitch pine-scrub oak (*Pinus rigida* and *Quercus ilicifolia*; Rice *et al.*, 2004), mixed pitch pine-white/black oak (*P. rigida*, *Quercus alba* & *Q. velutina*; von Holle *et al.*, 2013; Von Holle *et al.*, 2006) or Japanese black-pine (*Pinus thunbergii*; Taniguchi *et al.*, 2009). Most of these were evergreens or mixed

evergreen-deciduous which, while locally dominant, exhibit vastly different traits compared to deciduous trees like *Robinia* with drastic changes in humus forms and soil processes (Ponge, 2003).

Several of this studies also separated nitrogen into its different forms for analysis and found increased mineral nitrogen content (ammonium and nitrates; Landgraf *et al.*, 2005; Medina-Villar *et al.*, 2016; von Holle *et al.*, 2013) with, in all cases, a comparatively higher increase in nitrate content compared to the increase in ammonium content. Our own results also highlighted an increase in nitrate content under *Robinia* (both pure or mixed with natives) but only when compared to native *Quercus* plots with an unsignificant positive trend in the case of *Castanea* plots (Figure 24). A lack of differentiated annual litterfall amount, mentioned in the previous section, suggests that changes in soil nitrogen content are a result of differences in nitrogen input from degrading *Robinia* organic matter. Indeed, as seen previously there are important differences in leaf nitrogen content between the three considered tree species (Figure 22), including between the two natives, with the highest and lowest values found for *Robinia* and *Quercus*, respectively, and intermediate values for *Castanea*. Nitrification does not appear to have been impacted, however, as there are no differences compared to native plots although the trend is negative compared to *Quercus* control. This is peculiar considering increased nitrate content in the same plots and may suggest differences between short and long term consequences of the presence of *Robinia* although this cannot be tested here.

Conversely, we found a very different pattern concerning soil ammonium content with a generaly negative, though contrasted, response although only significative in two cases: mixed plots with a *Quercus* control and pure plots with a *Castanea* control (Figure 24). This contrasts with nitrate content where only compared to *Quercus* control plots did *Robinia* have an effect. It also contrasts with the litterature where increased ammonium content have been found in most cases (Landgraf *et al.*, 2005; Von Holle *et al.*, 2013; Medina-Villar *et al.*, 2016). Potential ammonification, on the other hand, was negatively affected in all cases except mixed plots with a *Castanea* control (Figure 24) with a particularly strong effect in pure plots with a *Quercus* control despite a change in ammonium content itself. Overall, increased nitrate content and decreased ammonium content would tend to suggest increased nitrification as it has been suggested, or measured, in previous work (Landgraf *et al.*, 2005; Medina-Villar *et al.*, 2016).

### ***4.3. Understory plant communities***

Based on the literature specific to *Robinia* and the more-general literature on nitrogen-fixing tree species we expected understory vascular plant communities to be drastically affected by replacement of native species with *Robinia*.

The overall lack of response of understory plant communities (i.e. taxonomic and functional richness, diversity and divergence) was unexpected as it is a frequent consequence of native tree species replacement by *Robinia* in different contexts (Peloquin & Hiebert, 1999; Rice *et al.*, 2004; Benesperi *et al.*, 2012; Kou *et al.*, 2016) although not always (Von Holle *et al.*, 2006; Akatov *et al.*, 2012; Sitzia *et al.*, 2012; Masaka *et al.*, 2013). Similarly, contrary to what has been suggested in the litterature we found no difference in overall biomass or plant cover per plot (Kou *et al.*, 2016). Due to the generally observed increase in soil nitrogen content *Robinia* has been found to favour nitrophilous species while hindering oligotrophic species (Benesperi *et al.*, 2012; Kou *et al.*, 2016) although it is not always true (Vasilopoulos *et al.*, 2007; Terwei *et al.*, 2016). In our study nitrophilous species such as blackberry (*Rubus fruticosus* L.), hedge nettle (*Stachys sylvatica* L.) or nettle (*Urtica dioica* L.) were unaffected in their cover or abundance by the presence of *Robinia* (unpublished data) despite increased soil total nitrogen content and, more importantly in this case, increased soil nitrate content (Figure 24). It is worth noting that even in plots with increased soil nitrate content (mixed and pure *Robinia* plots with *Quercus* control) absolute values remained low (28.2 ± 16.0 mg-$NO_3^-$.$kg^{-1}$) while beech plots of similar age within the same region had comparable values (29.6 ± 8.0 mg-$NO_3^-$.$kg^{-1}$; Trap *et al.*, 2011). This suggests that despite a relative increase compared to the corresponding control available nitrate remained too low for nitrophilous species to replace existing species. It has been suggested that *Robinia* is generally found in relatively nitrogen-poor areas due to increased competitive abilities or due to preferential plantation in such areas (Terwei *et al.*, 2016). Total plant biomass tended to increase in the same plots, which could have been attributed to increased nutrient availability, yet that highly variable depending on local conditions.

While functional diversity of plant communities was not affected by the presence or dominance of *Robinia* there were some changes in community-weighted average values for several traits most notably, functionally, leaf dry matter content and specific leaf area (SLA). The former decreased while the latter increased in monospecific *Robinia* plots compared to *Quercus*-dominated plots. Both these traits are considered to be predictors of plant resource acquisition and use strategies and, combined, reflect leaf thickness (Vile *et al.*, 2005). The main factors influencing SLA is nutrient and light availability (Cornelissen *et al.*, 2003) with the latter being linked to an adaptive response to competition for light. As such SLA is expected to generally decrease following opening of the canopy as is the case here in *Robinia* plots with a *Quercus* control (Table 6). Yet we observe the opposite with increased SLA couple with increased light availability suggesting that nutrient availability is the main driver of these changes, which is coherent with the increased nitrate content in these same plots (and similar trends in mixed plots). This will have a positive effect on understory plant fresh leaf and litter

for both herbivores and detritivores although, in the case of the latter, it is a rather minimal food source compared to tree leaf litter.

### *4.4. Bigger is better: differentiated responses of soil microarthropods and the macrofauna*

We sampled various groups of organisms within the soil fauna in order to assess for direct and indirect effects of *Robinia* on higher trophic level. Primary consumers in both detritivory- and herbivory-based food webs can be impacted by altered litter quantity, quantity or changes within understory plant communities, respectively. Secondary consumers are then susceptible to be affected by changes among primary consumers populations.

We found limited changes within soil macrofauna communities with an increase in species richness in *Robinia*-dominated plots when compared to native *Quercus*-dominated plots. A higher number of geophagous species (i.e. earthworms) and, to a lesser extent, phytophagous species notably among gastropods and isopods caused this increased richness. The species absent in native plots and present in *Robinia*-dominated plots, *Octolasion lacteum* and *Allolobophora chlorotica*, are both endogeic. As such, increased nutrient availability may have favoured such species or, alternatively by the increased soil humidity at the time of sampling which can increase earthworm activity-abundance. The moderate and insignificant increase in understory plant biomass may have also played a role through a higher fine root biomass. Overall, our results on the soil macrofauna support what has been previously observed in the few studies that have focused on the response of the soil fauna to replacement of native tree species by *Robinia*. The few that have focused on the soil macrofauna as a whole (Brygadyrenko, 2015; Buchholz *et al.*, 2015), only soil arthropods (Degomez & Wagner, 2001) or saproxylic beetles (Della Rocca *et al.*, 2016). Among them, most found no significant changes species richness or diversity (Brygadyrenko, 2015; Buchholz *et al.*, 2015; Della Rocca *et al.*, 2016). We found no change in taxonomic diversity yet observed decreased functional divergence and evenness in *Robinia*-dominated plots compared to *Castanea* native plots. The combination of both, coupled with a lack of change in functional richness, is characteristic of homogenised communities favouring more generalist species with intermediate trait values. This suggests that, when compared to native *Castanea* plots, plots dominated by *Robinia* tend to provide a less diverse habitats for the soil fauna thus narrowing the range of optimum trait values.

One particular study, comparing arthropod diversity under *R. pseudoacia* with *R. neomexicana* found a negative effect on diversity and species richness which, in this case, cannot be attributed to altered nitrogen cycling (Degomez & Wagner, 2001). They found, among other changes, a decrease in predator diversity while a decreased abundance was observed for soil chilopoda and formicidae as

well as changes in species composition of carabid beetles and spiders (Buchholz *et al.*, 2015). All these organisms are primarily predators yet we found no significant differences in abundance or diversity for zoophages in our study. However, we did find a decreased abundance of acari in *Robinia* plots (both mixed and pure) when compared to native *Quercus*. While acari as a whole encompass multiple trophic groups a large proportion of them are indeed predators (e.g. gamasid mites) or parasites (i.e. ticks).

Among these studies only the one by Buchholz et al (2015) considered soil microarthropods making these results the most novel of this study. In addition to the negative effect on acari abundance compared to native *Quercus*, we observed increased abundance of collembola (i.e. springtails) this time when compared to *Castanea*-dominated plots. While the results found by Buchholz et al (2015) for collembola were not significant the trend was also towards an increase in collembolan abundance under *Robinia* with the pioneer species *Betula pendula* (silver birch) as a native control. Collembola are known to be highly sensitive to desiccation, acidity as well as light, bulk density and porosity. While soil pH and soil humidity in these plots were unaffected there was a decrease in soil bulk density thus increasing the volume of coarse pores necessary for euedaphic (i.e. soil dwelling) and hemiedaphic (i.e. soil and litter dwelling) collembola to disperse, and establish themselves, within the soil. In addition, canopy cover also increased in these sites thus limiting understory irradiance and desiccative stress primarily for epiedaphic (i.e. litter dwelling) collembola. Furthermore, several studies highlight strong relationships between collembolan assemblages and microbial communities (Perez *et al.*, 2013), understory plants (Abgrall *et al.*, 2017; Henneron *et al.*, 2017) with legumes (Salamon *et al.*, 2004; Eisenhauer *et al.*, 2011). Despite the lack of changes in biomass within microbial and fungal communities, functional changes within these communities are to be expected particularly among nitrifying bacteria (both symbiotic and free-living). Such changes, combined with those of understory plants, could drive the observed response of collembolan assemblages. Multiple altered environmental variables susceptible to positively affect various groups of collembola may explain the lack of changes in functional diversity despite the positive response in abundance. Among the considered traits, many are related to soil habitat (i.e. layer) preference: furca length, body length, body shape as well as the presence of visual organs. If both euedaphic and epiedaphic collembola abundances are positively affected then functional diversity may not be impacted.

## 5. Conclusion

Our study showed, and confirmed, that *Robinia pseudoacacia* can alter soil properties of temperate forests normally dominated by *Quercus petraea* or *Castanea sativa*. These alterations were particularly noteworthy in relation to nitrogen cycling (total nitrogen, nitrate & ammonium content, potential ammonification) and soil fauna trophic structure with significant variations in microarthropod abundances. They were, however, highly species-specific and dependent on the considered native control species with, overall, greater differences between *R. pseudoacacia* plots and *Q. petraea* plots than between *R. pseudoacacia* and *C. sativa.* Understory plants and the microbial compartment were largely unaffected in this study contrary to what was expected from previous work on *R. pseudoacacia* outside of its native range. Overall, our results highlight the need to consider multiple control tree species in order to properly account for the effect of an introduced exotic tree in temperate forest ecosystems.

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# Chapitre 4 – Effets des métabolites secondaires de la Renouée du Japon (*Reynoutria japonica*) sur les réseaux trophiques du sol

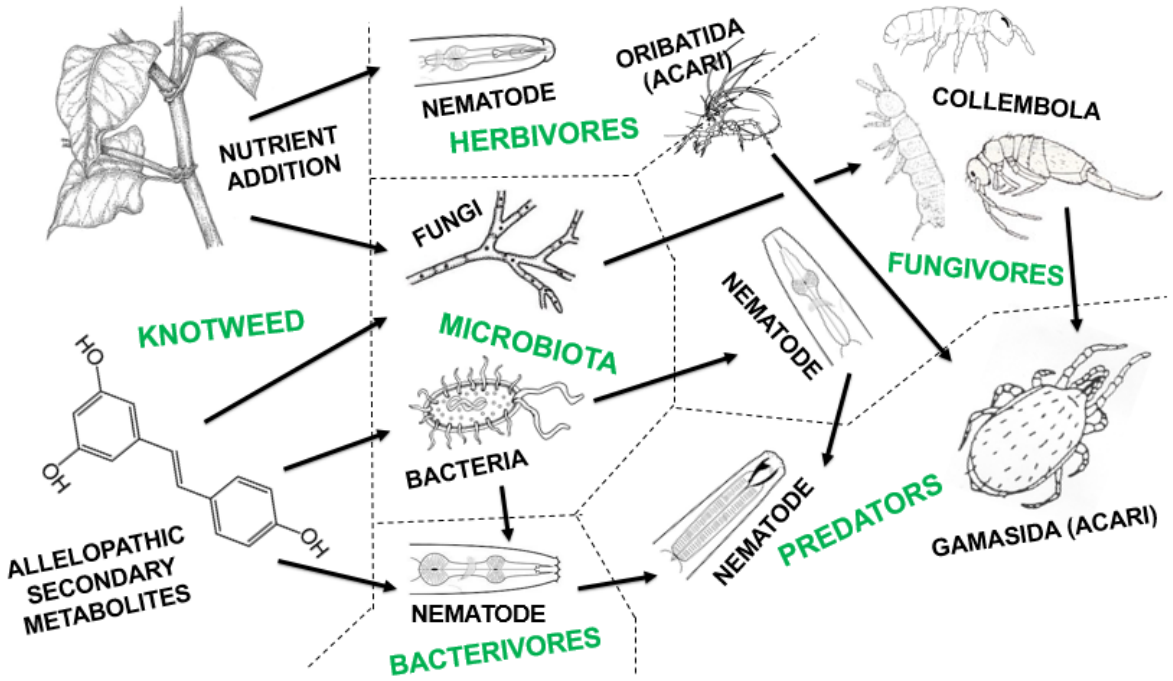


**Diagramme des groupes de la microflore, micro- et mésofaune du sol considérés dans ce chapitre**

# Invasion by Fallopia japonica alters soil food webs through secondary metabolites

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## Abstract

Biological invasions are a major threat to biodiversity with varying degrees of impact. There is increasing evidence that allelopathy often plays an important role in explaining both invasion success and impact on native taxa (e.g. novel weapons hypothesis). The effects of these secondary metabolites on plant communities and microorganisms are well known. However, their direct and indirect effects on soil fauna are unresolved, despite the importance of the latter in ecosystem processes and, potentially, invasion mitigation. Japanese knotweed (*Fallopia japonica*), an east-Asian species, which has proved to be invasive in Europe, containing allelopathic secondary compounds inhibiting native plants and microbial communities. The focal point of this study was the allelopathic effects of knotweed on soil mesofauna (Nematoda, Collembola and Acari). During a one-month laboratory experiment we added knotweed rhizome extract (KRE) at different concentrations to soils collected in an invasion-prone area. He experiment consisted of including or excluding secondary metabolites through the use of activated carbon filtration of KRE. This enabled us to separate effects caused by nutrient addition (i.e. trophic effects) and combined (trophic and allelopathic) effects. Relative effects of nutrient and secondary metabolites addition on abiotic and biotic soil variables were then quantified. We highlighted frequently contrasting trophic and allelopathic effects influenced in some cases by KRE concentration. Microbial assemblages, through fungal / microbial biomass ratio, did not show any congruent response to KRE secondary compounds but was more negatively impacted by nutrient addition. The use of a trophic-based path analysis led us to show that changes within the soil biota had repercussions on secondary consumers (e.g. bacterivorous nematodes and Collembola). Abundance within taxa at higher trophic levels such as predatory Acari (but not predatory nematodes) was also affected although to a lesser extent, likely in part due to the limited considered timeframe. Overall, we showed that, in controlled conditions, invasive allelopathic plants such as knotweeds can have effects on soil fauna at different trophic levels through addition of both nutrients and secondary metabolites to the soil. Considering the limited knowledge of allelopathic effects on the soil fauna and soil functions, this study provides new information on above- and belowground interactions.

*Keywords:* plant-soil interactions ; novel weapons hypothesis ; allelopathy ; trophic networks ; alien species

## 1. Introduction

Past and current introduction of invasive plant species and their spread in new ecosystems is a major concern for conservation at a global level (Pyšek *et al.*, 2012; Litt *et al.*, 2014) due to their severe impact on biodiversity (Murrell *et al.*, 2011; Vilà *et al.*, 2011) and ecosystem processes (Bassett *et al.*, 2011; Kohyt & Skubała, 2013). Only a small number of exotic species become invasive in their introduced range (Reinhart & Callaway, 2006) through distinctive characteristics (or traits) providing superior competitive ability when compared to native species (Van Kleunen *et al.*, 2010b). These traits can be morphological in nature by directly improving plant fitness (Van Kleunen *et al.*, 2010b) or physiological with the synthesis of biochemical, secondary metabolites that influence the germination, growth, survival and/or reproduction of other organisms (Inderjit *et al.*, 2011b).

The novel weapon hypothesis (NVH) suggests that the success of many exotic invasive plant species is due to the possession of allelopathic compounds unencountered by native species, particularly native plant species (Callaway & Ridenour, 2004). Furthermore, it has been shown that many invasive species have different allelopathic potential effects between their native and introduced ranges (Thorpe *et al.*, 2009; Inderjit *et al.*, 2011a). These biochemical compounds, exudated from plant roots (Callaway *et al.*, 2008) or released from degrading litter (Inderjit *et al.*, 2011a) have powerful effects on ecosystem functioning by impacting both organisms and ecological processes (Wardle *et al.*, 1998; Hättenschwiler & Vitousek, 2000; Reigosa *et al.*, 2006; Hättenschwiler *et al.*, 2011).

Under the soil, plants interact with a wide range of organisms including bacteria, fungi, nematodes and various kinds of arthropods (Parepa *et al.*, 2013; Abgrall *et al.*, 2017). These aboveground-belowground relationships can be antagonistic (e.g. herbivores, pathogens) or mutualistic (e.g. mycorrhizeous fungi, nitrogen-fixing bacteria) (Van der Putten *et al.*, 2007). Allelopathic biochemical that have a negative effect on plants can do so indirectly by promoting or inhibiting particular soil biota (Stinson *et al.*, 2006; Callaway *et al.*, 2008). Furthermore, the soil biota is known as having a structuring influence on plant community composition, dynamics and phenology (Wardle, 2002; Forey *et al.*, 2015), allelopathy feedback from the soil biota could further increase invasion (Parepa *et al.*, 2013).

Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr. 1988, Polygonaceae) was introduced in Europe in the 19$^{th}$ century for its ornamental properties. It is now one of the most destructive invasive species in Europe and North America (Lowe *et al.*, 2000). *F. japonica* spreads mostly by clonal rhizomatous growth with a single stem or rhizome node being able to regenerate a full plant explaining the high-dispersion capacity of knotweed (De Waal, 2001). Multiple species of the genus *Fallopia* such as *F. japonica, F. sachalinensis* as well as their hybrid *F.* ×*bohemica* are known to

contain and produce several secondary metabolites (Murrell *et al.*, 2011). Some of those compounds exhibit allelopathic properties and can inhibit the germination or growth of other plant species (Gerber *et al.*, 2008; Aguilera *et al.*, 2010) as well as bacteria (Hedenec *et al.*, 2014) with mixed effects on fungi (e.g. Daayf *et al.*, 1995; Kumagai *et al.*, 2005). A study by Vastano *et al.* (2000) revealed a higher concentration of stilbenes in North American invasive *F. japonica* than in Chinese native individuals of the same species tending to support the NVH in the case of knotweed. One of these compounds, *trans*-resveratrol (3,4,5'-trihydroxy-trans-stilbene), has been identified as being produced by knotweed (Vastano *et al.*, 2000). This molecule, which is also found in grapevines, is known as having antifungal (Filip *et al.*, 2003) and antibacterial properties (Chan, 2002). Content analysis of resveratrol in knotweed tissues has been assessed by Vaher & Koel (2003) who found that more than 80% of *trans*-resveratrol was located in the roots and rhizomes, where the majority of plant-microorganisms interactions occur (Bais *et al.*, 2006).

Secondary metabolites present in knotweed rhizomes could have either a direct effect on soil fauna either by repellence (Asplund *et al.*, 2015), toxicity (Isman & Duffey, 1982) or an indirect effect through changes in the soil biota (Ens *et al.*, 2009). As evidence for direct toxicity of phenolic compounds is scarce, indirect effects through alterations of basal resources for secondary consumers appear more likely. In this paper, we studied the effect of knotweed rhizome aqueous extracts on the soil biota and fauna in order to provide additional information on the novel weapon hypothesis in this particular case. Indeed, while several studies have assessed knotweed allelopathic potential in invaded areas none, as far as we know, have considered the impact on the soil fauna in relation to this hypothesis. Therefore and based on the theory, we hypothesized that: (i) knotweed has a negative effect on microbial (and particularly bacterial) biomass through rhizome allelopathic secondary metabolites ; (ii) this negative effect has repercussions on higher trophic levels through trophic cascades, and results in soil food web structure alteration ; (iii) this negative effect is be slightly attenuated by a positive trophic effect of nutrient addition provided by knotweed rhizome extract ; (iv) those effects, positive (i.e. trophic) or negative (i.e. allelopathic), are concentration-dependent.

## 2. Material & Methods

### *2.1. Material collection and experiment preparation*

Belowground *F. japonica* biomass was harvested in early autumn 2016 within a spontaneously invaded plateau site in Normandy, France (49.455024° N; 1.062645° W). To the best of our knowledge, control measures have never been applied to this site. Samples were kept in an icebox for transportation to the laboratory. Rhizomes were water-cleaned and stored at 4°C prior to extraction. We used an electric grinder to break plant tissues and facilitate osmosis. One hundred grams of ground

plant material was mixed with 1000 ml of distilled water. This aqueous extract was kept at 19°C for 24h. Following Norsworthy (2003) the mixture was then passed through a series of sieves ranging from 1000 to 50 µm and then vacuum filtered through standard filter paper (> 20-25 µm). The extract was then further sterilized by filtering through 0.22 µm filter.

We collected soil from the upper 10 cm of a reaped grassland in a small valley. While the area was uninfested by *F. japonica* close-by sites (< 200 m) with similar topographical and edaphic conditions have been invaded for several years. Macrofauna as well as macroscopic plant materials were removed from the collected soil. Samples were gently, and unforcefully, sieved at 5 mm so as to preserve mesofauna and mixed. Ten 200 g samples were taken from the soil to sample initial Collembola, Acari and Nematoda communities. Soils were placed in 8 x 8 x 10 cm plastic pots. Filter paper (<10-20 µm) was placed at the bottom of the prevent leakage of the pot content. Sixty grams of fine grained sand was added above the filter paper forming a ~ 0.5 cm layer. The rest of the pot was filled with 310 ± 5 g of soil. Ten 400 g samples of mixed soil were also collected for analysis of initial physico-chemical conditions. A layer of 0.5 g of *Agropyron* sp. litter, which is the dominant species in the samples grassland and also present close to invaded sites, was added to provide physical habitat for the soil fauna. Pots were kept at 19 °C in a phytotron with a 8 h day / 16 h night cycle for a week. In order to increase and homogenize abundance and compensate for possible losses during soil sieving each pot was then placed under 2 individual Berlese-Tullgren extractors, one containing topsoil (0 – 5 cm) and the other deeper soil (5 – 10 cm) from the same area.

### ***2.2. Experimental design***

To simulate varying natural conditions and test for concentration-dependence distilled water was used to provide different concentrations of the aforementioned aqueous KRE (0, 33, 66 & 100%). Half of the solution at each concentration, including distilled water, was filtered 3 times through activated carbon prior to watering. This filtration was conducted in order to remove potentially toxic organic compounds (Cheremisinoff & Ellerbusch, 1978) from the KRE. We also filtered distilled water in order to test for the effect of filtration itself.

In total, we obtained 8 different solution: filtered and unfiltered distilled water, filtered and unfiltered 33% KRE, filtered and unfiltered 66% KRE as well as filtered and unfiltered 100% KRE. Each solution was used to water 10 pots prepared as detailed above. The result was a balanced factorial design (4 x 2 x 10 = 80 pots with 10 replicates per modality). During the experiment, the pots were kept for four weeks (from early November to early December 2016) in a climate-controlled room (21.0 ± 1.9°C, 16h day / 8h night, 47.0 ± 8.8 % humidity) and watered weekly with the corresponding solution.

### *2.3. Sampling, biochemical analysis and fauna identification*

In order to verify the validity of our activated-carbon methodology we used HPLC to test for resveratrol concentration in filtered and unfiltered KRE. Resveratrol ($C_{14}H_{12}O_3$), a phenolic allelopathic compound, was measured using direct-injection high-performance liquid chromatography (ThermoFisher Scientific UltiMate 3000 UHPLC). We used a variable wavelength UV detector at 306 nm, equipped with a standard C18 column, a water-acetonitril (60:40) mobile phase and an isocratic flow of 1 $ml.min^{-1}$ (Goldberg *et al.*, 1994). We used commercially-available Resveratrol powder (CAS Number: 501-36-0) for calibration.

At the end of the experiment several biotic and abiotic variables were assessed. Approximately 100g of fresh soil was used for springtail extraction in a Berlese-Tullgren funnel (Macfadyen, 1961). Samples were weighted and placed within sieves (stitch: 1 mm, diameter: 80 mm, height: 50 mm) above a plastic funnel. Extraction, under a heat source, lasted for a week with individuals collected in 70% ethanol. This extraction method is dependent on the limited tolerance of these animals to desiccation and will therefore only extract active individuals. There is therefore no differentiation between individuals that were inactivated, killed or otherwise incapacitated. One hundred grams of fresh soil was used for nematode extraction in a Baermann funnel (McSorley & Walter, 1991). Dampened samples were placed in a porous paper (10-15 µm stitch) supported by a 2 mm sieve and placed above a water-filled and sealed funnel for 48h. This method has a limited efficiency in isolating slow moving and nematodes and will not isolate inactive individuals (Van Bezooijen, 2006) and thus is not exhaustive.

Mesofauna samples were separated into Acari and Collembola under a stereo binocular microscope. Collembola individuals were mounted in lactic acid on microscope slides for identification with a phase-contrast optical microscope. Collembola individuals were identified to the species level (Potapov, 2001; Thibaud, 2004; Hopkin, 2007). Acari were identified to the order or suborder level: Mesostigmata (Gamasida), Cryptostigmata (Oribatida) and Prostigmata (Actinedida) (Coineau & Cleva, 1997). The cohort Astigmatina (previously the suborder Astigmata) were included in the suborder Oribatida (Wang & Fan, 2010). After Baermann funnel extraction, nematodes were counted while active under a stereo binocular microscope. Following decantation nematodes were fixed using a 4% formaldehyde solution and mounted on microscope slides. Individuals were attributed to trophic groups (herbivores, bacterivores, fungivores and predators/omnivores) based on mouthpart examination under a compound optical microscope.

Four grams of fresh soil were used to measure soil ergosterol content using the method proposed by Gong, Guan & Witter (2001). Ergosterol is a sterol found within fungi and protozoa.

Ergosterol concentration can be used as a proxy of soil fungal biomass. Two times 20 g of fresh soil was used to assess microbial biomass using chloroform fumigation and extraction (Brookes *et al.*, 1985). Carbon extraction was performed in 100 ml of potassium sulphate 0.05 M ($K_2SO_4$) for chloroform-fumigated or unfumigated samples.

Once springtail extraction was complete a 30 g dry soil aliquot used to assess soil abiotic variables. Soil pH was measured using 1:5 volumetric fraction in 1 M potassium chloride (KCl) using a Mettler Toledo FiveEasy pH meter. Total carbon and nitrogen content was measured in a ThermoFisher Flash Analyzer 2000 after electric grinding of dry soil material.

### ***2.4. Statistical analysis***

We used ANOVA tests included in R Software 3.3.1 for statistical analysis. In order to assess for knotweed rhizome extracts (KRE) effect on the soil fauna and microbiology we calculated the relative differences between the considered modalities and our control by standardizing and normalizing our measured values in relation to control means. This was done by subtracting the average control value to each value for the considered modality. Based on our methodology and hypotheses we considered that several of the potential effects of KRE could be separated. We thus considered that subtracting the control mean to values obtained in modalities where KRE was unfiltered by activated carbon (AC) values gave the combined effect of KRE on the considered variable (Figure 26). Based on the generally accepted hypothesis we considered that AC filtration retains knotweed secondary compounds. Therefore, subtracting control means to values measured in pots subjected to AC filtered KRE we calculated KRE effect not attributable to secondary metabolites (Figure 26). We referred to this effect as a trophic effect that could directly affect soil microbiology by adding nutrients to the substrate with potential indirect repercussions on higher trophic levels. Finally, the same methodology was used by subtracting for each concentration the mean AC filtered value to individual values measured in pots that received unfiltered KRE.

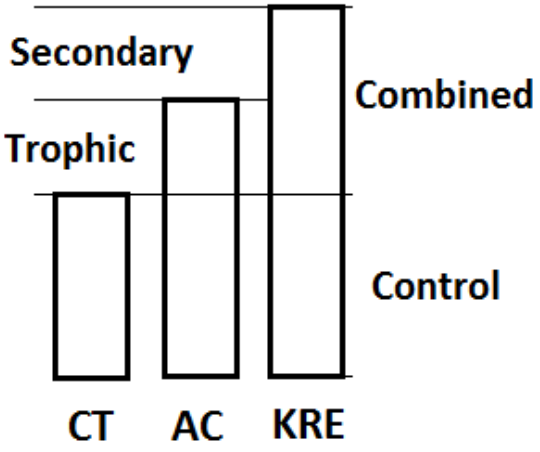


*Figure 26: Diagram of calculations involved in separating knotweed rhizome extract (KRE) effects. CT: control, AC: activated carbon filtration, KRE: no AC filtration.*

We used a null model approach in order to consider control stochastic variability. Null vectors were randomly generated for each variable based on the observed distribution parameters of the

control. Significant differences between these null vectors and our data vectors was assessed using non-parametric Wilcoxon signed-rank test. An iterative procedure (one-thousand repetitions) and result aggregation enabled us to robustly, and conservatively, assess for statistical differences between control and treatments. These differences, when found, showed KRE effects on the considered variables.

We also assessed for differences in the structure of the soil food web with and without AC filtration, and thus with or without knotweed secondary metabolites. We used multigroup path analysis to model our empirically observed model and compare it to a "null" multigroup model. The "null" model had constrained intercepts and regression coefficients that was compared to the empiracl model using ANOVA. This approach provides a means to assess for covariating responses of soil fauna compartments to potential allelopathy.

## 3. Results

### *3.1. Physico-chemistry & microbiology*

Contrary to our hypothesis and the literature, we observed limited effect of knotweed rhizome extracts (KRE) on microbiological variables. There were no significant differences in ergosterol concentration, an indicator of fungal biomass, irrespective of concentration or filtration mainly due to high variability. Regarding microbial carbon, a proxy of overall microbial biomass, nutrient addition seems to cause a decrease as concentration increases but insignificantly except at intermediate concentrations (-10.74 ± 4.04 %; $p < 0.05$; Table 8) with repercussions on ergosterol / microbial ratio (17.25 ± 6.06 ; $p < 0.05$; Table 8). pH was also affected by KRE addition with a significant decrease in response to secondary metabolites addition at the lowest concentration (-0.02 ± 0%; $p < 0.05$; Table 8) which shifted to an increase at the highest concentration (+1.38 ± 0.5; $p < 0.05$; Table 8). The C/N ratio remained largely unaffected by KRE input except at the highest concentration (combined effect: - 1.37 ± 0.56 %; $p < 0.05$; Table 8).

Resveratrol concentration for 100% v/v KRE was 2.27 ± 0.23 $mg.l^{-1}$ while the literature suggests an $IC_{50}$ (i.e. concentration for 50% mortality) of 9 $mg.l^{-1}$ (Fan *et al.*, 2010). We did not detect resveratrol in any detectable amount in KRE samples after activated carbon filtration, even at the highest concentrations. Several chromatograms detailing these analysis are provided in Appendice D.

*Table 8: Relative differences in physico-chemical and microbiological variables compared to control values (%) between knotweed rhizome extract exposed pots and control pots. Values are means +/- SE. P-values are from repeated Wilcoxon rank-sum tests on absolute relative differences.*

| *Percentage differences from control* | *33% v/v* | | | *66% v/v* | | | *100% v/v* | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Combined* | *Nutrient* | *Secondary* | *Combined* | *Nutrient* | *Secondary* | *Combined* | *Nutrient* | *Secondary* |
| Ergosterol content | 8.05 ± 6.97<br>n.s. | 1.88 ± 4.69<br>n.s. | 0.06 ± 0.07<br>n.s. | 4.75 ± 4.97<br>n.s. | 8.99 ± 4.99<br>n.s. | -3.89 ± 4.56<br>n.s. | 3.86 ± 4.26<br>n.s. | 0.11 ± 7.16<br>n.s. | 3.75 ± 4.25<br>n.s. |
| Microbial carbon | -4.2 ± 6.11<br>n.s. | -4.29 ± 6.18<br>n.s. | 0 ± 0.06<br>n.s. | -7.78 ± 5.91<br>n.s. | **-10.74 ± 4.04**<br>**p < 0.05** | 3.32 ± 6.63<br>n.s. | -5.31 ± 6.55<br>n.s. | -11.38 ± 8.87<br>n.s. | 6.84 ± 7.39<br>n.s. |
| Ergosterol / Microbial C ratio | 10.98 ± 11.32<br>n.s. | 3.98 ± 7.48<br>n.s. | 0.07 ± 0.11<br>n.s. | 10.81 ± 7.52<br>n.s. | **17.25 ± 6.06**<br>**p < 0.05** | -5.5 ± 6.42<br>n.s. | 9.17 ± 9.67<br>n.s. | 24.16 ± 22.81<br>n.s. | -12.07 ± 7.79<br>n.s. |
| pH (KCl) | -1.05 ± 0.48<br>p < 0.10 | **1.39 ± 0.4**<br>**p < 0.01** | **-0.02 ± 0**<br>**p < 0.05** | 0.93 ± 0.46<br>p < 0.10 | 0.39 ± 0.43<br>n.s. | 0.53 ± 0.46<br>n.s. | 0.48 ± 0.49<br>n.s. | **-0.89 ± 0.29**<br>**p < 0.05** | **1.38 ± 0.5**<br>**p < 0.05** |
| C/N ratio | -0.18 ± 0.55<br>n.s. | -0.52 ± 0.49<br>n.s. | 0 ± 0.01<br>n.s. | 0.11 ± 0.67<br>n.s. | 0.64 ± 0.6<br>n.s. | -0.52 ± 0.67<br>n.s. | **-1.37 ± 0.56**<br>**p < 0.05** | -0.07 ± 0.57<br>n.s. | -1.3 ± 0.57<br>p < 0.10 |

## ***3.2. Nematodes***

Total nematode abundance showed a strong response to KRE input at all concentrations despite important differences in effect direction. For instance, total nematode abundance was reduced by half following addition of low-concentration KRE (Figure 27; Table 9). Conversely, nematode abundance was almost doubled at the highest KRE concentration while no response was found at the intermediate concentration (Figure 27; Table 9). This general trend (i.e. combined KRE effect) is the result of decreasing intensity and significance of responses to nutrient addition (from +86 % at minimum concentration to +21 % at maximum concentration; Figure 27; Table 9) and highly contextual responses of nematodes to secondary compounds addition (from -43 % at intermediate concentration to +48 % at maximum concentration; Figure 27; Table 9).

Although significance and intensity differed, bacterivorous and fungivorous nematodes (41.07 ± 1.59 % and 22.35 ± 1.26 % of total nematodes abundance, respectively) response to KRE addition varied similarly to the general trend with a shift from a negative (-43.5 % / -79.8 %) to a positive (+58.3 % / +24.5 %) response with increasing KRE concentration (Table 9). Herbivorous nematodes abundance (28.0 ± 1.3 % of total abundance) varied somewhat differently with a significant, and positive, response to KRE addition only at the highest concentration (+177 % increase; Table 9). Nutrient addition appeared to elicit a generally positive response independently of concentration (+64.8 ± 17.6 %) which was only significant at the highest concentration (+59.2 ± 21.3 %; Table 9) while there was no significant response to secondary compounds addition. Predatorous and omnivorous nematodes showed no significant response to KRE addition (Table 9).

*Table 9: Relative differences in nematode abundances between knotweed rhizome extract exposed pots and control pots. Values are means percentages of difference +/- SE. P-values are from repeated Wilcoxon rank-sum tests.*

| *Percentage differences from control* | *33% v/v* | | | *66% v/v* | | | *100% v/v* | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Combined* | *Nutrient* | *Secondary* | *Combined* | *Nutrient* | *Secondary* | *Combined* | *Nutrient* | *Secondary* |
| Total abundance | **-43.52 ± 15.76** | **86.29 ± 25.72** | -0.7 ± 0.08 | -14.29 ± 15.97 | **50.78 ± 19.34** | **-43.15 ± 10.59** | **80.22 ± 29.05** | 21.59 ± 21.95 | 48.22 ± 23.89 |
| | **p < 0.05** | **p < 0.01** | n.s. | n.s. | **p < 0.05** | **p < 0.01** | **p < 0.05** | n.s. | p < 0.10 |
| Bacterivores | -43.52 ± 20.78 | 59 ± 34.27 | -0.64 ± 0.13 | -27.64 ± 15.05 | 54.43 ± 25.03 | **-53.14 ± 9.75** | **58.3 ± 21.49** | 12.19 ± 36.48 | 41.11 ± 19.15 |
| | p < 0.10 | n.s. | n.s. | n.s. | p < 0.10 | **p < 0.001** | **p < 0.05** | n.s. | p < 0.10 |
| Herbivores | 16.12 ± 23.1 | 69.23 ± 32.53 | -0.31 ± 0.14 | 43.93 ± 33.55 | 66.01 ± 38.26 | -13.3 ± 20.21 | **177.12 ± 60.86** | **59.19 ± 21.25** | 74.09 ± 38.23 |
| | n.s. | p < 0.10 | n.s. | n.s. | n.s. | n.s. | **p < 0.05** | **p < 0.05** | p < 0.10 |
| Fungivores | **-79.83 ± 5.26** | **138.03 ± 43.19** | -0.92 ± 0.02 | **-49.79 ± 12.07** | 6.67 ± 18.76 | **-52.93 ± 11.32** | 24.52 ± 28.52 | -16.06 ± 18.97 | 48.35 ± 33.98 |
| | **p < 0.0001** | **p < 0.05** | n.s. | **p < 0.01** | n.s. | **p < 0.01** | n.s. | n.s. | n.s. |
| Predators/omnivores | -18.82 ± 19.73 | -39.64 ± 24.42 | 0.34 ± 0.33 | -8.71 ± 28.14 | 42.23 ± 33.72 | -35.81 ± 19.78 | 47.14 ± 35.15 | 34.69 ± 52.25 | 9.24 ± 26.1 |
| | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |

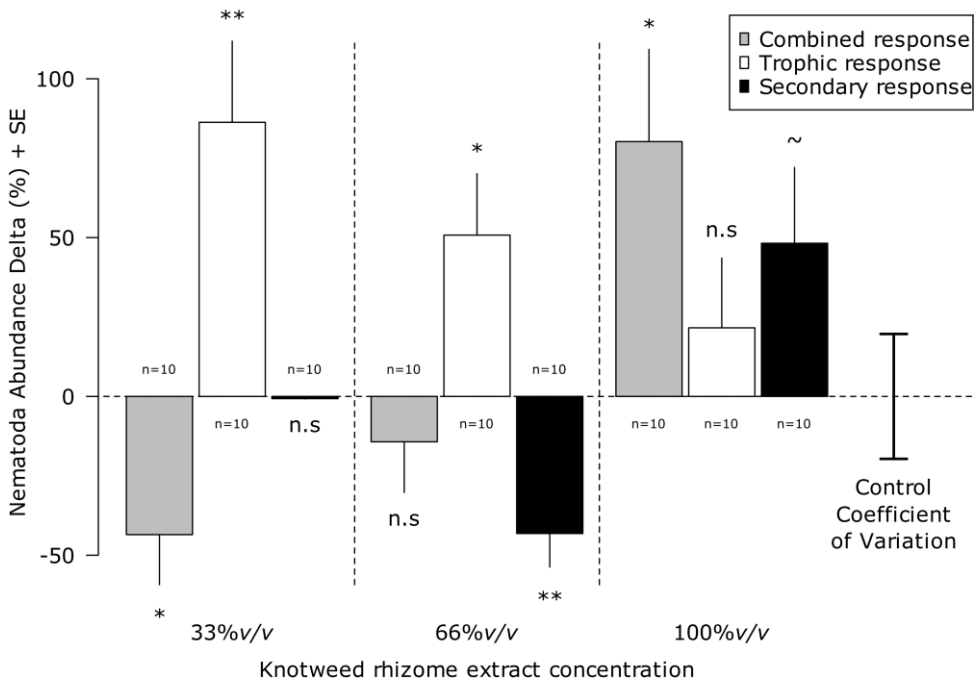


*Figure 27: Relative nematode total abundance (%) compared to control in relation to knotweed rhizome extract dilution levels and activated carbon filtration with decomposition of effects. Symbols indicate levels of significativity of repeated statistical testing of differences between calculated values and null generated controls. n.s.: p > 0.10, ~ : p < 0.10, * : p < 0.05, ** : p < 0.01, *** : p < 0.001, **** : p < 0.0001.*

### 3.3. Mesofauna

*Table 10: Relative differences in mesofauna (Collembola and Acari) abundance, taxonomic and functional indices between knotweed rhizome extract exposed pots and control pots. Values are means +/- SE. P-values are from repeated Wilcoxon rank-sum tests.*

| | *Percentage differences from control* | *Combined* | *33% v/v Nutrient* | *Secondary* | *Combined* | *66% v/v Nutrient* | *Secondary* | *Combined* | *100% v/v Nutrient* | *Secondary* |
|---|---|---|---|---|---|---|---|---|---|---|
| Acari | Total abundance | **138.1 ± 40.88** | 46.67 ± 22 | 0.62 ± 0.28 | **176.19 ± 33.75** | 77.14 ± 41.05 | **55.91 ± 19.05** | **223.81 ± 47.26** | 25.71 ± 39.47 | **157.58 ± 37.59** |
| | | **p < 0.01** | p < 0.10 | n.s. | **p < 0.001** | p < 0.10 | **p < 0.05** | **p < 0.01** | n.s. | **p < 0.01** |
| | Predators | **73.58 ± 30.4** | 24.53 ± 16.92 | 0.39 ± 0.24 | **133.96 ± 30.71** | 13.21 ± 20.28 | 106.67 ± 27.13 | 35.85 ± 28.79 | 13.21 ± 31.82 | 20 ± 25.43 |
| | | **p < 0.05** | n.s. | n.s. | **p < 0.01** | n.s. | p < 0.01 | n.s. | n.s. | n.s. |
| | Herbo-fungivors | **203.85 ± 65.99** | 69.23 ± 39.39 | 0.8 ± 0.39 | **219.23 ± 71.16** | 142.31 ± 77.57 | 31.75 ± 29.37 | **415.38 ± 77.39** | 38.46 ± 53.85 | **272.22 ± 55.89** |
| | | **p < 0.05** | n.s. | n.s. | **p < 0.05** | p < 0.10 | n.s. | **p < 0.001** | n.s. | **p < 0.001** |
| Collembola | Total abundance | 73.85 ± 52.25 | 67.69 ± 39.35 | 0.04 ± 0.31 | **93.85 ± 28.85** | 56.92 ± 28.35 | 23.53 ± 18.38 | **66.15 ± 27.79** | 12.31 ± 31.03 | 47.95 ± 24.74 |
| | | n.s. | n.s. | n.s. | **p < 0.01** | p < 0.10 | n.s. | **p < 0.05** | n.s. | p < 0.10 |
| | Shannon's diversity | **57.54 ± 22.41** | 43.05 ± 28.93 | 0.1 ± 0.16 | **109.41 ± 20.98** | 51.9 ± 34.08 | **37.86 ± 13.81** | 19.82 ± 27.1 | **79.26 ± 21.71** | -33.16 ± 15.12 |
| | | **p < 0.05** | n.s. | n.s. | **p < 0.001** | n.s. | **p < 0.05** | n.s. | **p < 0.01** | p < 0.10 |
| | Functional richness | 24.93 ± 34.62 | 15.61 ± 22.45 | 0.08 ± 0.3 | **70.38 ± 27.46** | 5 ± 32.7 | **62.26 ± 26.15** | -40 ± 27.42 | 13.5 ± 29.19 | -47.14 ± 24.15 |
| | | n.s. | n.s. | n.s. | **p < 0.05** | n.s. | **p < 0.05** | n.s. | n.s. | p < 0.10 |
| | Functional eveness | -5.3 ± 4.13 | -0.85 ± 4.7 | -0.04 ± 0.04 | **-8.88 ± 3.46** | 1.26 ± 3.98 | **-10.02 ± 3.42** | -1.31 ± 5.2 | -1.61 ± 4.33 | 0.31 ± 5.28 |
| | | n.s. | n.s. | n.s. | **p < 0.05** | n.s. | **p < 0.05** | n.s. | n.s. | n.s. |

Total Acari relative abundance showed a strong positive response to KRE input at all concentrations without significant differences in intensity (from +138.1 to +223.8 % as concentration increased; Figure 28) which appears to me mostly related to a response to secondary compounds addition. A similar pattern was observed for oribatid mites (Table 10). There were significant differences between responses at the lowest and highest concentration levels for both the combined and secondary compounds responses but not for response to nutrient addition (Table 10). Predators (i.e. mostly Gamasida) abundances responded only to the combined aspects of KRE addition, and only at the two lowest concentrations (Table 10).

Regarding Collembola abundance observed response patterns are positive although only significative when considering combined KRE effects at intermediate and high concentration (+93.9 and +66.2 %, respectively; Figure 29). A positive, yet unsignificant, effect of nutrient addition seems to exist at the intermediate concentration (+56.9 ± 28.4 %; $p < 0.10$; Table 10). Taxonomic diversity (i.e. Shannon's diversity) responded positively to KRE addition (only significant at the two lowest concentrations). A response (positive) to secondary compounds was only found at the intermediate KRE concentration (Table 10). Collembola functional richness and evenness, calculated using trait data from the COLTRAIT database (Salmon & Ponge, 2012; Salmon *et al.*, 2014), only responded at 66% v/v KRE, mainly linked to the secondary allelopathic effect of KRE addition. Functional evenness decreased while functional richness increased in both cases (Table 10).

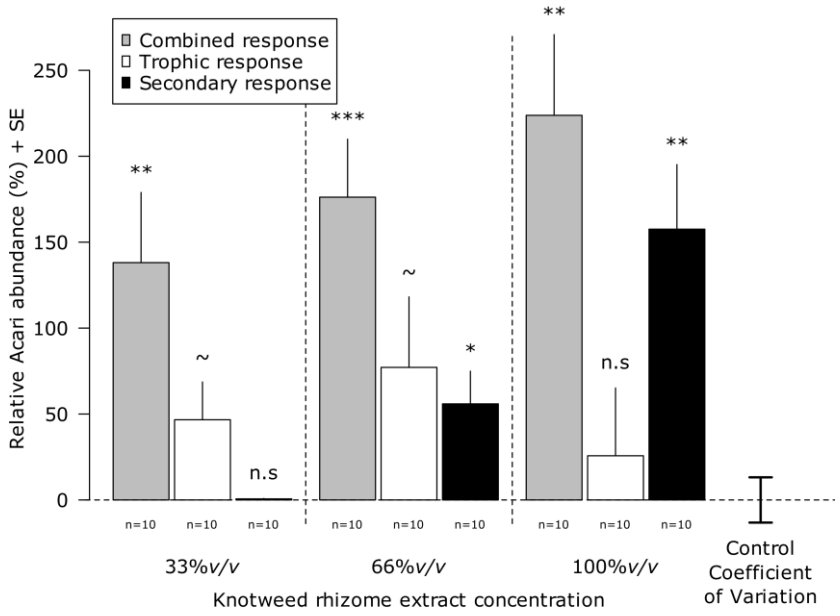


*Figure 28: Relative Acari total abundance compared to control in relation to knotweed rhizome extract dilution levels and activated carbon filtration with decomposition of effects. Symbols indicate levels of significativity of repeated statistical testing of differences between calculated values and null generated controls. n.s.: p > 0.10, ~ : p < 0.10, * : p < 0.05, ** : p < 0.01, *** : p < 0.001, **** : p < 0.0001.*

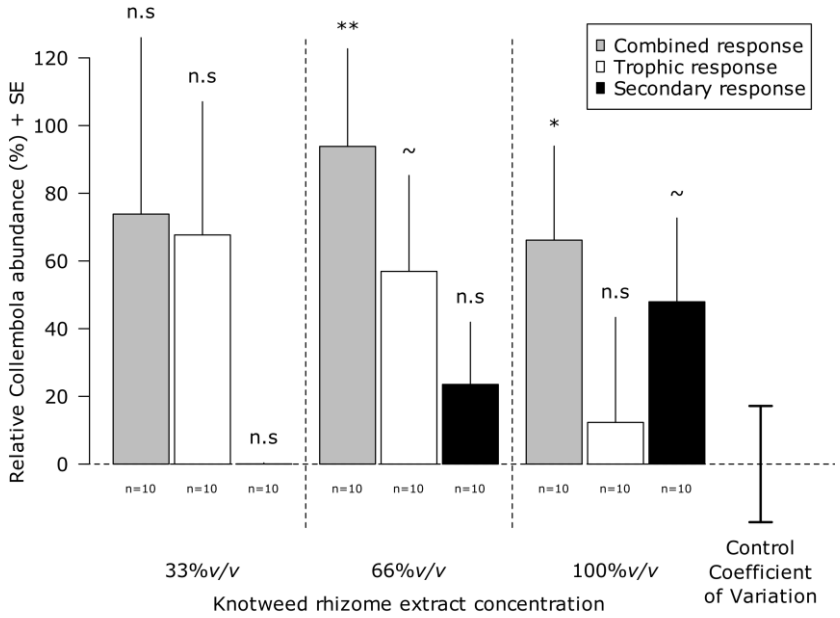


*Figure 29: Relative Collembola total abundance compared to control in relation to knotweed rhizome extract dilution levels and activated carbon filtration with decomposition of effects. Symbols indicate levels of significativity of repeated statistical testing of differences between calculated values and null generated controls. n.s.: p > 0.10, ~ : p < 0.10, * : p < 0.05, ** : p < 0.01, *** : p < 0.001, **** : p < 0.0001.*

### ***3.4. Path analysis***

Differences between the empirically observed and a "null" multigroup model with constrained intercepts and regression coefficients was tested using ANOVA. It showed a difference in model structure between the two groups (i.e. unfiltered and activated carbon filtered KRE addition) ($n_{group1}$ = 40, $n_{group2}$ = 40, $Chi^2$ difference = 39.87, $p$ = 0.022).

Allelopathic effect removal through activated carbon (AC) filtration increased the strength of the relationship between KRE concentration and microbial carbon concentration (From -0.005 p = 0.816 to -0.032 p = 0.048; Figure 30) and the effect of the latter on Collembola abundance (-6.998 p = 0.384. to -14.443 p = 0.060; Figure 30), herbo-fungivorous Acari abundance (4.217 p = 0.530. to -9.884 p = 0.075; Figure 30) and bacterivorous nematodes abundance (0.864 p = 0.941. to -25.575 p = 0.027; Figure 30). The relationship between bacterivorous and predatorous nematodes abundance remained unaffected by AC filtration (0.126 p = 0.000. to 0.111 p = 0.000; Figure 30). The relationship between herbo-fungivorous and predatorous Acari abundance was not significantly altered by AC filtration (0.030 p = 0.593. to 0.089 p = 0.176; Figure 30).

Concerning the fungal pathway pathway allelopathic effect removal through activated carbon (AC) filtration decreased the relationship, yet with still no significant relationship, between KRE concentration and fungal biomass (i.e. ergosterol concentration) (0.013 $^{p = 0.174.}$ to -0.007 $^{p = 0.571}$; Figure 30). Fungal biomass relationships with its consumers was also affected by allelopathic effect removal: with herbo-fungivorous Acari (18.681 $^{p = 0.166.}$ to -3.119 $^{p = 0.693}$; Figure 30), Collembola abundance (-1.464 $^{p = 0.928.}$ to 17.470 $^{p = 0.118}$; Figure 30) and, in a very limited way, fungivorous nematodes abundance (-1.973 $^{p = 0.836.}$ to 8.794 $^{p = 0.274}$; Figure 30). Strengths of relationships of these taxa with their predators also changed after allelopathic effect removal especially fungivorous nematodes (-0.213 $^{p = 0.011}$ to -0.067 $^{p = 0.348}$; Figure 30) and Collembola (0.126 $^{p = 0.009}$ to -0.050 $^{p = 0.282}$; Figure 30) with predatorous Acari. The relationship between fungivorous and predatorous nematodes abundance was mostly unaffected (-0.030 $^{p = 0.593}$ to 0.089 $^{p = 0.176}$; Figure 30) as was the relationship between the two main predatorous groups (i.e. predatorous nematodes and Acari) (0.244 $^{p = 0.161}$ to -0.119 $^{p = 0.496}$; Figure 30).

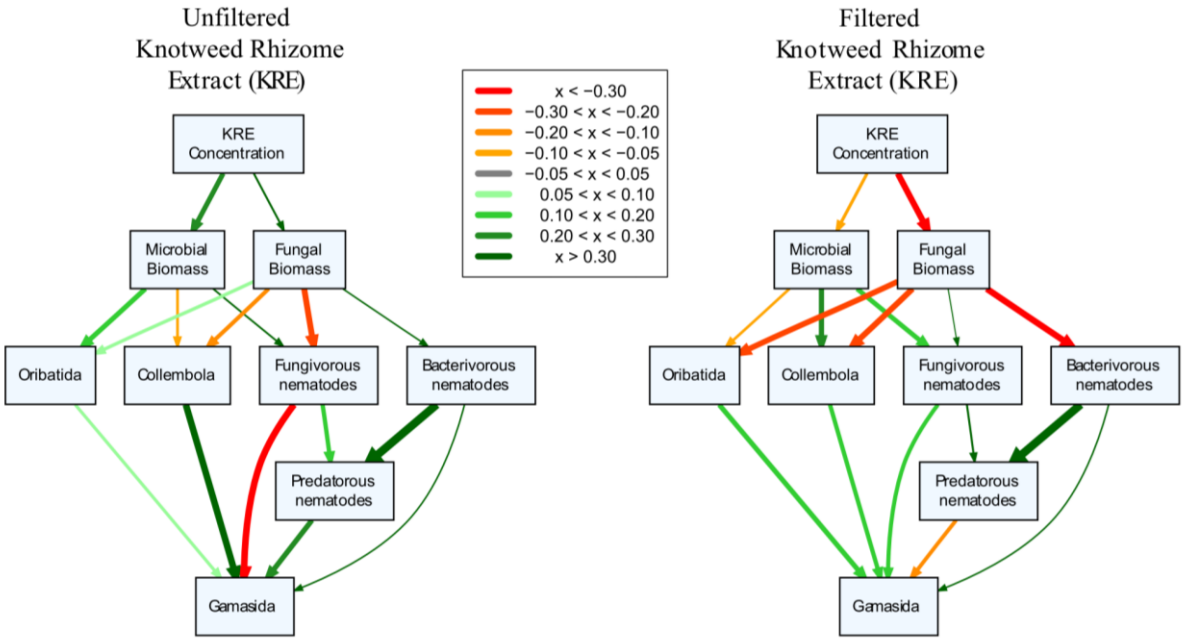


*Figure 30: Multigroup path model of soil mesofaunal food webs after filtered or unfiltered knotweed rhizome addition. Differences between the observed multigroup model and a "null model" with fixed Intercepts and Regressions was assessed with an ANOVA. Green arrows indicate a positive correlation while red arrows indicate a negative correlation. Arrow width is proportional to the strength of the relationship. KRE concent. = knotweed rhizome extract concentration level, Fungi = ergosterol concentration, Microbial Biomass = carbon amount in microbial biomass, Fungiv. nemat. = Fungivorous nematodes abundance, Bacter. nemat. = Bacterivorous nematodes abundance, Predat. nemato. = Predatorous nematodes abundance, Herb.-Fung. Acari = Herbo-fungivorous Acari, Predat. Acari = Predatorous Acari, Collemb.= Collembola.*

## 4. Discussion

The first hypothesis posited a negative effect of knotweed allelopathic secondary compounds (ASC) on microbial communities as generally observed *in situ* (Hedenec *et al.*, 2014; Tamura & Tharayil, 2014). The effect of ASC addition was not directly tested on the soil fauna, due in part to the lack of a proper identification of all such potential compounds in knotweed (Fan *et al.*, 2010). However, we were able to ascertain the removal of ASC from a solution of knotweed rhizome extract (KRE) by using activated carbon which is known to suppress allelopathic effects (Ridenour & Callaway, 2001 but see Lau *et al.*, 2008 for a critic of this methodology). We were able to test and demonstrate removal of one ASC, trans-resveratrol, from KRE through activated carbon filtration (Appendice D). Differences in population responses between activated carbon filtered and unfiltered KRE addition to the soil was therefore considered to be mainly, but not only, due to removal of ASC. We then indirectly calculated a "secondary" effect of KRE. Contrary to our hypothesis, we generally did not find any significant antimicrobial effects on ergosterol concentration (a proxy of fungal biomass; Davis & Lamar, 1992), microbial carbon (a proxy of microbial biomass; Vance *et al.*, 1987) or the ratio between the two (a rough indicator of microbial community structure; Djajakirana *et al.*, 1996; Table 8). Ergosterol concentration itself remained unaffected by KRE at concentrations which is consistent with the contrasting, yet often positive, effects found in the literature on the effects on fungal biomass (Daayf *et al.*, 1995; Lecerf *et al.*, 2007; Tamura & Tharayil, 2014). The pro-microbial, albeit insignificant, effects are far more surprising and tend to refute our hypothesis and contrast with results found in the literature (Kumagai *et al.*, 2005; Hedenec *et al.*, 2014; Tamura & Tharayil, 2014; Stefanowicz *et al.*, 2016). Most of these results were observed in the field, with multiple potential confounding factors, with only Daayf *et al.*, 1995 and Kumagai *et al.*, 2005 directly testing antimicrobial and antifungal properties of knotweeds secondary compounds in controlled conditions. For instance, a major source of knotweed allelopathic properties are linked to the slow degradation and release of phenolic compounds from leaf litter degradation (Lavoie, 2017) which we did not account for in this study. Overall while the antibacterial effect of knotweeds in general, and Japanese knotweed in particular, appear fairly conclusive in the literature our results tend to show that this cannot be attributed to, or only to, rhizome secondary metabolites.

The final hypothesis stipulated that knotweed KRE-addition effects, in particular ASC addition, were linearly concentration-dependent. This hypothesis cannot be properly segregated from the other and will be considered here to avoid repetition. This hypothesis was based on the literature which frequently mentions release of secondary metabolites in the environment by knotweeds as a major contributor to knotweed effects in their invasive range (Vastano *et al.*, 2000). Other lab studies have shown concentration-dependent effects of some root-secreted phenolic compounds on microbial

biomass (e.g. Zhang *et al.*, 2015). These compounds; however, are not in the same family as resveratrol or catechin. We tested this hypothesis indirectly as the effect of secondary metabolites was calculated and not measured. Concerning the concentration-dependence of microbiological response to ASC the relationship remained unsignificant in all cases for both fungal and microbial biomass (Table 8). Hence, while there may be concentration-dependence the effects themselves are unsignificant, and we must therefore accept the alternative hypothesis in the case of ASC. Nutrient addition, however, significantly and negatively affected microbial biomass at 66% v/v concentration only, showing differences dependent on concentration. However, as this is for intermediate concentration there does not appear to be a linear relationship between concentration and response. When analyzing changes in soil food web structure we showed that allelopathic secondary compounds (ASC) removal increased the strength of the negative correlation between KRE concentration and microbial biomass, the corollary being that ASC addition would tend to decrease the strength of the relationship between the two (Figure 30). Only after ASC removal was the relationship significant between the two variables. Therefore, while the combined, and ASC, effects on microbial biomass appear not to be concentration-dependent purely "trophic" effects are significantly so.

The second hypothesis stated that, if there were antimicrobial and antifungal effects of KRE, they would have repercussions on higher trophic levels through a trophic cascade with potential alterations of trophic structures. We showed previously that no antimicrobial or antifungal effect were found in our experiment in response to KRE of allelopathic secondary compounds (ASC). However, the evidence revealed significant differences in abundance at higher trophic levels. Indeed, we did find significant effects of KRE on bacterivorous and fungivorous nematodes (both positive and negative) abundances as well as herbo-fungivorous Acari and Collembola abundances (mostly positive) from both allelopathic or combined effects (although with no consistent pattern at different concentrations; see Tab 2-3). We found no significant differences in predator nematodes abundances despite the changes in abundance of their prey. Predator Acari, on the other hand, had higher abundances following KRE addition. Accordingly, predators may have had a top-down effect on microbivores while being unaffected themselves by bottom-up regulation themselves in the considered timeframe. Unfortunately, we could not find any reports in the literature on nematodes abundances under knotweed and therefore cannot assess the representativity of our results. Skubala & Mierny (2009), on the other hand, found a significant negative effect of giant knotweed (*Fallopia sachalinensis*) on oribatid mites (mostly herbivores, fungivores or both) but no effect on Collembola abundance (mostly generalist fungivores and detrivores). They attributed observed effects in the field on liberation phenolic compounds from leaf litter degradation, not rhizome excretion. This is, to our knowledge, the only publication to date assessing knotweed effects on the soil mesofauna in spontaneously invaded

sites. Hedenec *et al.* (2014) also considered Collembola and Acari, with mixed results and no differences with native species, but in an agricultural setting with giant knotweed used as a biofuel crop. Macroarthropod abundance, which we did not consider in this study, has generally been shown to be negatively affected by knotweed presence (Kappes *et al.*, 2007; Gerber *et al.*, 2008; Topp *et al.*, 2008)

Collembola and Acari have a generation time of several weeks to months, depending on taxa and eco-morphological group (Joosse & Veltkamp, 1969; Verhoef & Selm, 1983; Choi *et al.*, 2002; Prinzing *et al.*, 2002; Park, 2007; Ermilov & Lochynska, 2008). Observed differences are thus unlikely to be caused by a predator-prey intergenerational regulation but would be due to a more direct effect. Predatory nematodes and Acari have generation times ranging from 3 to 280 days depending on taxa (Ydergaard *et al.*, 1997; Abou-Awad *et al.*, 2001; Khan *et al.*, 2007) as well as temperature. For some taxa within our study the experiment duration, 1 month, may have been insufficient to observe significant repercussions on higher trophic levels through intergenerational predator-prey relationships.

We also assessed how activated carbon filtration, and thus ASC removal, affected the structure of the soil trophic network by using multigroup path analysis (Figure 30). The comparison of an empirical model to a constrained model, clearly showed that ASC removal significantly altered overall relationships between the various considered faunal groups. In this analysis, ASC removal also seemed to more readily alter relationships between taxa in the microbial food web (i.e. between microbial biomass and abundances of Collembola, oribatid mites and bacterivorous nematodes). This relationship was, however, negative. This would suggest that ASC removal from added KRE increases the interdependency of compartments/taxa within the microbial food web as well as the effect of KRE concentration on microbial biomass. The corollary, although we did not test it directly, would be that the allelopathic component of knotweed effect tends to limit between-group variability. In addition, it would appear that while nutrient input has concentration-dependent effects (at least on microbial biomass), nutrient and allelopathic effects are not dependent on concentration. Another striking feature is the change in the relationship between fungivorous nematodes and predatorous Acari, for which intensity was drastically reduced by ASC removal from KRE and most importantly switched from a negative to a positive correlation.

We also posited that part of knotweeds success as invaders was due to lack of adaptation by native species to the invader: the novel weapon hypothesis (Callaway & Ridenour, 2004). This framework most generally applies to other plant species with which there is more direct competition. While our methodology does not enable us to assess that effect, we expected negative effects (on

abundance and diversity) of knotweed allelopathy on at least some taxa within the soil fauna which would help explain results found in several field studies (Kappes *et al.*, 2007; Gerber *et al.*, 2008; Topp *et al.*, 2008; Skubala & Mierny, 2009). Such negative effects could have been direct through phytotoxicity or indirect through a trophic cascade or changes in habitat structure. This was not the case here with few negative responses of soil fauna to ASC addition. The only significant negative effects documented were for all types of nematodes in response to 66% KRE addition (Table 9).

The third hypothesis centered on the posited countering of negative allelopathic effects of KRE addition by nutrient addition. This appears to be the case, albeit unsignificantly, for the ergosterol / microbial C ratio at the two highest concentrations which is negatively affected by the allelopathic component of KRE (i.e. favoring microbial biomass) and positively affected by the nutrient-addition component (i.e. favoring fungal biomass) with a combined positive effect. Field studies evaluating fungal:bacterial ratios have found conflicting results on that matter with both increased (Tamura & Tharayil, 2014; Suseela *et al.*, 2016) and decreased (Stefanowicz *et al.*, 2016) ratios under knotweed-invaded plots. The results tend to support the first case of decreased bacterial biomass, although fungal biomass remained unaffected (Table 8). These effects of knotweed are often attributed to increased litter biomass (e.g. Suseela *et al.*, 2016) and changes in litter chemistry (higher litter C/N ratios: Dassonville, Guillaumaud, Piola, Meerts, & Poly, 2011; Mincheva *et al.*, 2014; Urgenson, Reichard, & Halpern, 2009; higher litter lignin content: Aguilera *et al.*, 2010) in addition to the already mentioned allelopathic effects. Our decomposition of effects between nutrient and secondary compounds addition tends to indicate that this positive effect on fungal:microbial ratios is mainly attributed to a positive response of microbial biomass to increased nutrient input to the soil. Due to lack of leaf litter this is not comparable to field nutrient input, but nonetheless worth considering. Secondary compounds, which can be twice as concentrated in knotweed-invaded plots (Suseela *et al.*, 2016), appear to have a negative effect on fungi:microbial biomass ratios in this case. Changes in microbial biomass carbon have the most influence over shifts in this ratio in our case (i.e. negative effect of nutrient-addition and positive effect of secondary compounds addition) which would to be contrary to our hypothesis. The pH responded in a similar manner with a significant negative nutrient addition effect, a significant positive secondary compounds effect but an unsignificant slightly positive combined effect. A decrease in soil pH has generally been observed in field studies (Kappes *et al.*, 2007; Dassonville *et al.*, 2008, 2011) and is also attributed to increased litter biomass in knotweed stands. This is, however, not always the case (Stoll *et al.*, 2012; Stefanowicz *et al.*, 2017)

Finally the results regarding microarthropod abundances (i.e. Collembola and Acari) are ambiguous with no evidence of the hypothesized pattern of attenuating effects. In fact, all significative responses of both Acari and Collembola are positive. This would seem, contrary to our hypothesis, to

indicate a synergetic combined effect of KRE addition (mostly at intermediate and high concentrations). In all cases of significant response to a combined effect one or both components' response was neutral (nutrient addition especially). Contrasting and inverse results from nutrient and secondary metabolites addition have also been found for nematodes at intermediate KRE concentration with a negative ASC addition effect, positive nutrient addition effect and neutral combined effect. Direct nematocidal effects of plant secondary compounds have been documented in some cases, mostly in laboratory studies (Chitwood, 2002). If there was such a direct effect of knotweed we would expect it to also be present at the highest concentration, which is not the case in our study (Figure 27).

These results provide the basis for further research on knotweed such as more detailed characterization of knotweed ASC and their potential allelopathic effects as well as further field work. As assessment of indirect, and direct, allelopathic effects of phenolic compounds on soil fauna has rarely been done. Thus, this report should provide useful data for authors working on such a subject as information is currently scarce on the subject. Finally, we hope the results presented here will provide useful reference data for future biological invasions study and inform managers of invaded areas on knotweed potential impacts.

## 5. Conclusion

In conclusion, the results showed an effect of knotweed rhizome extract (KRE) on soil microbiology. Fungal biomass remained unaffected but microbial biomass as a whole responded negatively to KRE in some cases. Interestingly these negative responses, when they occurred, were mostly attributable to factors other than the allelopathic secondary compounds (ASC) within KRE, most notably nutrient addition. Calculated responses of microbial biomass to ASC addition were, albeit unsignificantly so, positive. While KRE addition had an effect in most cases on taxa "higher" within the soil trophic networks, there were no evident and generalizable trophic cascades across trophic levels for a given KRE concentration. Path analysis did reveal important changes in soil food web structure (constructed based on hypothesized producer-consumer relationships) which appeared to be mostly within the bacterial pathway, and concentration-dependent. There was circumstantial, but not generalizable, evidence of compensating, or attenuating, effects of nutrient and ASC addition on various taxa. Rarely was ASC effect, when documented, concentration-dependent in the results.

## Aknowledgements

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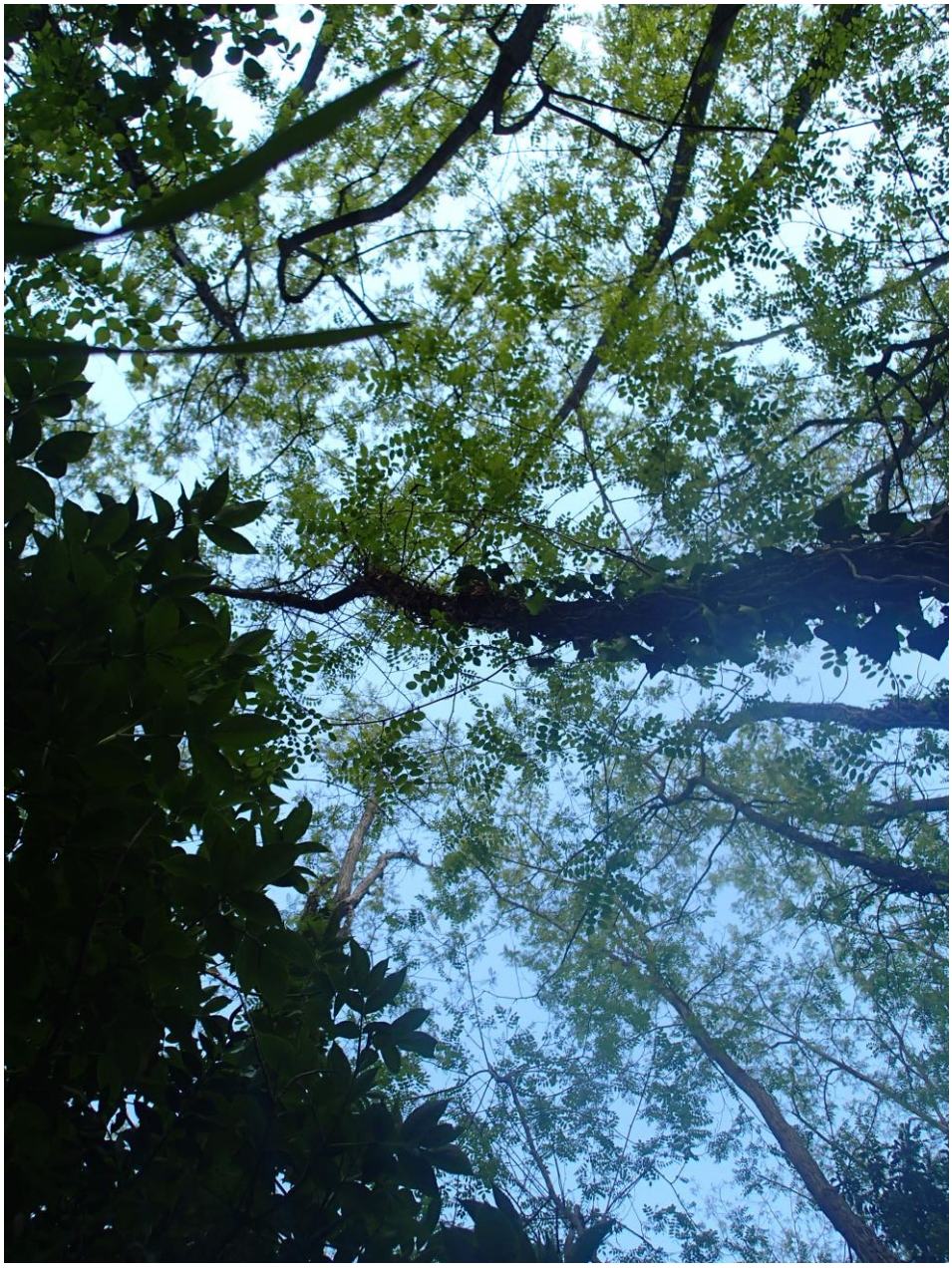
# Discussion générale



**Canopée du robinier faux-acacia en Espagne en début de saison estivale**

## 1. Considérations générales

Les travaux réalisés dans le cadre de cette thèse et présentés ici ont pour objectif d'approfondir les connaissances sur l'impact des invasions biologiques sur la faune du sol, la végétation native et leur substrat. Pour cela plusieurs études ont été réalisés à différentes échelles grâce à une synthèse de la littérature et à des études de cas sur deux plantes exotiques et envahissantes le robinier faux-acacia (*Robinia pseudoacacia*) et la renouée du japon (*Reynoutria japonica*).

L'envahissement par des plantes exotiques naturalisées est connu pour son potentiel transformateur sur les écosystèmes en affectant les communautés végétales et animales ainsi que sur le fonctionnement de l'écosystème en lui-même (Hejda *et al.*, 2009; Ehrenfeld, 2010; Pyšek *et al.*, 2012; Litt *et al.*, 2014; McCary *et al.*, 2016; Zhang *et al.*, 2018). Les connaissances acquises aux cours des dernières décennies ont fait drastiquement progresser le domaine, tant par l'étude de très nombreux cas pratiques que par le développement d'un cadre théorique général. La construction de ce cadre formel général s'est principalement focalisés sur les causes des invasions biologiques et les mécanismes sous-jacents à la transition entre naturalisation et envahissement (Richardson *et al.*, 2003; Blackburn *et al.*, 2011). La formalisation de la définition de ce que constitue « l'impact » d'une invasion biologique est plus récente encore (Jeschke *et al.*, 2014). Ce cadre théorique propose de considérer plusieurs points dans la prise en compte de l'impact :

Comment la **direction** de l'impact est-elle considérée ? Par exemple, concernant le robinier faux-acacia, considère t'on l'hypothèse unidirectionnelle, et donc orientée, d'un impact négatif sur la diversité végétale des communautés de sous-bois ou l'hypothèse bidirectionnelle, et neutre, d'une altération de la composition des communautés ? La première option fait sens d'un point de vue purement orienté vers l'analyse du risque lié aux invasions biologiques mais peut amener à une absence de prise en compte d'effets positifs potentiels, ou de la complexité de la dynamique des écosystèmes. Une hypothèse unidirectionnelle peut être pertinente quand elle concerne une variable précise, et que les justifications biologiques sont fortes. C'est le cas, par exemple, de l'hypothèse d'une eutrophisation du milieu par augmentation de la teneur en azote en lien avec le remplacement d'essence native par le robinier faux-acacia, un arbre fixateur d'azote. Les répercussions potentielles sur les communautés végétales et surtout animales sont complexes et multifactorielles et l'impact ne peut ici être défini simplement en « positif » et « négatifs ».

Est-ce que la **classification** et la **quantification** des impacts est bien neutre, traitant simplement de la direction et de la magnitude du changement observé, ou considère-t-elle des critères subjectifs liés à la perception et aux intérêts anthropiques ? Comme mentionné en introduction la

définition même de ce qui constitue l'impact d'une espèce exotique envahissante, ou « invasive » est sujette à débat entre différents acteurs. Différentes organisations de réglementation internationales incluent dans la définition d'une espèce exotique envahissante la notion d'un impact négatif socio-économique et écologique (DAISIE, 2006; EPPO, 2019; IUCN, 2019). La communauté scientifique, en revanche, prend en compte uniquement les propriétés dispersives et de maintien dans le temps (Richardson *et al.*, 2003; Blackburn *et al.*, 2011). L'existence d'un impact, s'il en est, est considérée séparément, et de manière objective par la notion d'espèce « transformatrice ». Comme proposé par Jeschke *et al.* (2014), il est nécessaire de séparer la magnitude de l'effet, objective et quantifiable écologiquement, des conséquences socio-économiques et de la valeur accordée par l'humain à cet effet. Les deux formant « l'impact » au sens large.

Quelle est l'**échelle spatiale** de l'impact considéré (locale, régionale, continentale, globale, etc) ? Est-elle propre à un type de milieu, d'habitat ou d'écosystème particulier ? Qu'en est-il de l'**échelle temporelle** de l'impact (temporaire ou permanente) ? Selon l'échelle considérée la nature et la perception de l'effet d'une invasion biologique peut changer du tout au tout, tant dans sa magnitude que dans ses conséquences écologiques et socio-économiques.

Les résultats présentés dans la discussion traitent uniquement de la quantification de l'impact des invasions biologique et de manière neutre. Il s'agit principalement d'impacts bidirectionnels car impliquant plusieurs variables pouvant varier indépendamment. Les éléments suivant sont discutés selon les hypothèses présentées en introduction : (i) l'impact des invasions biologiques sur la faune du sol, (ii) le cas du robinier faux-acacia à l'échelle régionale et continentale, (iii) le cas de la renouée du japon et son effet sur les réseaux trophiques du sol et (iv) la conclusion générale de ce travail de thèse et les perspectives futures.

## 2. Discussions sur les hypothèses posées

### *2.1. Les invasions biologiques et la faune du sol*

**H1** : *Les invasions biologiques, de par leur présence et leur effet sur les écosystèmes, ont un impact fort sur les communautés de la faune du sol.*

La première hypothèse visait à confirmer l'existence d'un impact fort et clair à l'échelle globale des invasions biologiques sur la faune du sol, et de le quantifier, en considérant uniquement la magnitude et la direction de l'effet. Les synthèses précédentes sur la faune épigée (Litt *et al.*, 2014; McCary *et al.*, 2016) et endogée (Zhang *et al.*, 2018) laissaient supposer, pour la faune du sol dans son ensemble, un effet plutôt négatif mais mitigé par plusieurs facteurs. Les résultats présentés dans le Chapitre 1, ceux considérant uniquement l'abondance totale de la faune du sol, indiquent une absence de réponse à l'envahissement par des espèces exotiques. La tendance, non significative, est même plutôt vers une réponse positive. Ces résultats ne semblent pas être en accord avec l'hypothèse fréquente, dans des études de cas locales, d'une réponse négative de la faune du sol (p. ex. Morriën *et al.*, 2012; Tanner *et al.*, 2013; Maceda-Veiga *et al.*, 2016).

La richesse spécifique et la diversité n'ont été considérés dans cette méta-analyse (Chapitre 1). En effet, il n'aurait pas été possible de tester l'effet des modérateurs (c.-à-d. structure de l'habitat et groupes trophiques impactés) sur ces variables au vu du faible nombre d'études disponibles. Un test réalisé sur l'ensemble des données de richesse spécifique et basé sur 18 cas indique l'existence d'une réponse négative, mais limitée, de la richesse spécifique aux invasions biologiques végétales [log-response ratio (lnR) :-0,154 ± 0,098, t = -2.25 p = 0.038]. Une diminution de la richesse spécifique sans diminution de l'abondance suggère la disparition locale d'espèces plus rares, et donc une diminution de la diversité.

Malgré le fait que la faune du sol dans son ensemble ne soit pas impactée, les résultats obtenus par modélisation démontrent l'importance de le prise en compte de différents facteurs, dont l'habitat, dans la compréhension de l'impact des invasions biologiques végétales.

**H1.1** : *Les communautés de la faune du sol occupant des habitats distincts fonctionnent différemment, modérant la réponse aux invasions biologiques végétales.*

Plusieurs études ont montré (Gerber *et al.*, 2008; McCary *et al.*, 2016), ou suggéré (Litt *et al.*, 2014), des réponses différenciées de la faune du sol et/ou épigée entre différents types de milieux. Des synthèses spécifiques à un type milieu donné (p. ex. milieu forestier : Liebhold *et al.*, 2017). De plus, la littérature met en évidence plusieurs cas d'invasibilité différenciée entre types d'habitats pour une même espèce exotique (p. ex. *Heracleum* sp. *;* Pyšek & Pyšek, 1995; Renčo & Baležentienė, 2015) et des répercussions différentes sur la faune du sol, notamment en fonction de leur groupe trophique (p. ex *Reynoutria* spp. en milieux ripariens herbacés ou arbustifs ; Gerber *et al.*, 2008 ; et *Heracleum sosnowskyi* en milieux ouverts et fermés ; Renčo & Baležentienė, 2015).

Les résultats obtenus ici par méta-analyse confirment de manière claire ces résultats (Chapitre 1). Les différents modèles construits à partir de la taille de l'effet au sein des études individuelles montrent que la structure de l'habitat envahit (c.-à-d. ouvert *vs* fermé) est un très bon prédicteur de l'effet des invasions biologiques sur l'abondance de la faune du sol : positif en milieu fermé (c.-à-d. habitat forestiers ou arbustifs denses) et neutre à tendance négative en milieu ouverts (c.-à-d. habitats à faible densité en arbres et arbustes généralement dominés par des herbacées). Les communautés de la faune du sol des habitats forestiers tendent à avoir une redondance fonctionnelle moindre qu'en milieux ouverts (Tews *et al.*, 2004; Winck *et al.*, 2017). Elles pourraient alors être plus sensibles aux changements induits par l'invasion biologique à la fois sur les communautés végétales (p. ex. Hejda *et al.*, 2009; Pyšek *et al.*, 2012) et le sol (p. ex. Liao *et al.*, 2008; Ehrenfeld, 2010). L'augmentation de l'abondance totale, portée principalement par celle des détritivores (Figure 15), laisse supposer une réponse indirecte à l'envahissement au travers d'une altération de la quantité, qualité ou phénologie de la litière.

**H1.2** : *Cette réponse pouvant dépendre de la nature de l'interaction des organismes du sol avec l'envahisseur, les réponses diffèrent ainsi selon le groupe trophique considéré.*

Des nombreuses études de cas (p. ex. Morriën *et al.*, 2012; Tang *et al.*, 2012; Gutiérrez-López *et al.*, 2014; Motard *et al.*, 2015) appuyés par une méta-analyse récente (Zhang *et al.*, 2018) ont démontré des différences de réponse en fonction du groupe trophique considéré au sein de la faune du sol. La méta-analyse de Pei Zhang *et al.* (2019) démontre une augmentation importante de l'abondance des organismes détritivores et microbivores, associée à une augmentation de la biomasse bactérienne, au sein de la litière. Les résultats obtenus dans le cadre de cette thèse sont extraits d'études primaires majoritairement distinctes (8 études communes avec Zhang *et al.* sur 41 retenues dans la méta-analyse ; Appendice B), tendent également à confirmer une tendance générale à l'augmentation de l'abondance des détritivores, sans que cette augmentation soit significative. Les microbivores, en revanche, ne semblent pas dans le cas présent impactées par la présence d'espèces exotiques envahissantes. Au sein de la rhizosphère d'espèces exotiques, Pei Zhang *et al.* (2019) démontrent une diminution de l'abondance des herbivores et des prédateurs. Les résultats obtenus ici par méta-analyse ne confirment pas ces résultats, aucun effet marqué n'ayant été observé.

Les différentes modélisations produites à partir des données extraites de la littérature (Appendice B) montrent que le groupe trophique des organismes impactés, seul, ne suffit pas à expliquer la réponse de l'abondance aux invasions biologiques (Chapitre 1). En intégrant la structure de l'habitat envahit au modèle, le groupe trophique permet en revanche d'améliorer de manière significative la capacité du modèle à expliquer la réponse de la faune du sol. Il y a alors une réponse différenciée entre consommateurs primaires et secondaires. Les consommateurs primaires (herbivores et détritivores) sont ainsi positivement affectés dans leur abondance en milieu fermé, mais pas en milieu ouverts. Ces résultats suggèrent une régulation des communautés animales, dans le contexte des invasions biologiques, par la production primaire (c.-à-d. régulation trophique ascendante). Les consommateurs secondaires (microbivores et prédateurs) ne sont pas affectés par la présence d'espèces exotiques envahissantes, indépendamment de leur habitat. Les résultats de Zhang *et al.* (2019) démontrent des effets contrastés des invasions biologiques sur la biomasse bactérienne, augmentant dans la litière mais diminuant dans la rhizosphère. L'absence de différenciation entre les deux types de communauté (de la litière et de la rhizosphère) animale dans la méta-analyse présentée en chapitre 1 pourrait expliquer l'absence de changements dans l'abondance des microbivores. L'augmentation de l'abondance des proies potentielles devrait, en théorie, encourager un

accroissement de la taille de la population ce qui a été observé à de nombreuses reprises (Tallamy, 2004; Mgobozi *et al.*, 2008; Wolkovich *et al.*, 2009; Tanner *et al.*, 2013; Motard *et al.*, 2015). Les modifications induites dans la structure de l'habitat par les espèces exotiques envahissantes pourraient ici impacter négativement les prédateurs en perturbant les opportunités de chasse (Gerber *et al.*, 2008; Schirmel *et al.*, 2011), les deux mécanismes inverses aboutissant à une absence d'effet.

En conséquence les résultats obtenus ici ne permettent pas de valider complètement cette sous-hypothèse. Différents groupes trophiques répondent assez clairement de manière distinctes, au vu des tendances observées. En revanche, sans prendre en compte le type d'habitat dans lequel ces organismes vivent cette information, seule, ne semble pas être en mesure de prédire l'effet des invasions biologiques sur la faune du sol.

### ***2.2. Le robinier faux-acacia : cas d'étude à large échelle sur un arbre exotique fixateur d'azote en milieu forestier***

**H2** : *Le robinier faux-acacia, altère le fonctionnement des écosystèmes forestiers et affecte les communautés végétales natives et la faune du sol.*

Le robinier faux-acacia tend à posséder des caractéristiques fonctionnellement distinctes de celles des essences natives dans ses zones d'invasion (Figure 22; Grotkopp & Rejmánek, 2007; Luo *et al.*, 2016). L'association symbiotique qu'il réalise avec des bactéries rhizobiennes est relativement rare dans les forêts tempérées (Steidinger *et al.*, 2019) et le différencie des essences natives par un enrichissement du milieu en azote (Rice *et al.*, 2004; Landgraf *et al.*, 2005; Taniguchi *et al.*, 2007; Akamatsu *et al.*, 2011), par la production d'une litière de haute qualité nutritive (Rahmonov, 2009; Medina-Villar *et al.*, 2015; Luo *et al.*, 2016) ou directement par exsudation racinaire (Fustec *et al.*, 2009). Ces données relatives aux traits n'ont pas été mesurée sur nos sites d'études mais extraites d'une base de donnée (TRY Plant Trait Database ; Kattge *et al.*, 2011). Au-delà de la qualité chimique plus élevée des feuilles des feuilles, ces analyses révèlent une surface foliaire spécifique (SLA) plus importante ainsi qu'une teneur foliaire en matière sèche moindre corroborant les résultats observés dans une étude en Chine (Luo *et al.*, 2016). Une SLA plus importante tend à favoriser la compétition pour la lumière et permet une rentabilité photosynthétique accrue par unité de masse (Reich *et al.*, 1998). Cette augmentation est commune chez les espèces exotiques (Gulías *et al.*, 2003) et observée chez *R pseudoacacia* (Luo *et al.*, 2016). Ceci suggère des entrées plus importantes à la fois d'azote, bien connues (Rice *et al.*, 2004; Landgraf *et al.*, 2005; Medina-Villar *et al.*, 2015), mais aussi de carbone, dans l'écosystème.

Nos propres observations sur le terrain, à l'échelle Européenne, tendent à contredire en partie ces observations (Chapitre 2). Un enrichissement du sol en azote, et plus particulièrement en nitrate (Figure 18), a bien été observé. Cette augmentation reste relativement faible par rapport aux valeurs avancées dans la littérature dans d'autres contextes (Facteur 3 ; Medina-Villar *et al.*, 2016 ; Facteur 15-25 ; Rice *et al.*, 2004; Von Holle *et al.*, 2013). Il n'y a pas eu en revanche de changement dans la teneur en carbone, organique ou totale, dans le sol. La diminution observée du ratio C/N du sol est imputable à l'augmentation de la teneur en azote et non à des changements dans la teneur en carbone. Aucune différence dans la teneur en ammonium des sols, entre parcelles dominée par *Quercus* et celles dominées par le robinier, n'a été observée à large échelle. Certains auteurs ont montré une forte

variation saisonnière dans la teneur en azote minéral (ammonium et nitrate), les différences les plus importantes ayant été observées à la fin de l'été (Rice *et al.*, 2004; Pereira *et al.*, 2011). Ces valeurs élevées correspondrait alors à la dégradation rapide de la litière florale (riche en azote et représentant 6 % du total annuel) dont le pic de dépôt est estival (Medina-Villar *et al.*, 2015). Il est donc probable que l'échantillonnage réalisé dans le cadre de cette étude, uniquement au printemps, ait été insuffisant pour pleinement appréhender l'effet du robinier sur le cycle de l'azote.

L'ammonification et la nitrification potentielle n'ont été déterminées qu'à l'échelle de la Normandie et non Européenne (Chapitre 3). Les résultats obtenus démontrent une diminution forte de l'ammonification en présence du robinier mais pas de changement significatif dans la nitrification qui semble néanmoins tendre à diminuer, surtout par rapport au chêne sessile. Les résultats présentés dans la littérature sont contrastés à ce sujet. Rice *et al.* (2004) démontrent une augmentation massive du taux net de nitrification et de la minéralisation totale de l'azote par rapport aux parcelles natives (mélange de pin et de chêne) tout au long de l'année. Pereira *et al.* (2011) observent également une augmentation du taux net de nitrification, et de minéralisation totale de l'azote, par rapport aux parcelles natives (merisier), mais uniquement à certaines périodes (février-avril et juillet-septembre). Le taux net d'ammonification, lui, n'augmente qu'entre juillet et septembre (Pereira *et al.*, 2011). La phénologie particulière de la sénescence du robinier explique probablement ces variations saisonnières en apportant une quantité importante de matière organique riche en azote sous forme de fleurs lors de la période estivale (Medina-Villar *et al.*, 2015). Il parait là encore probable que l'échantillonnage uniquement printanier réalisé ici ne soit pas à même d'appréhender pleinement les modifications induites par le robinier dans le cycle des nutriments en milieu forestier.

Les changements dans les propriétés de la litière produites, augmentant leur qualité nutritive et leur palatabilité, tendent bien à accroitre la décomposition de la litière. Une diminution importante de l'épaisseur des horizons organiques (OL, OF, OH) a bien été observée à l'échelle du gradient (Figure 18). Les analyses plus complètes en Normandie (Chapitre 3) ont aussi montré une accélération de la décomposition de la litière et une augmentation de la respiration potentielle (Figure 25). Ces observations ne peuvent être directement confirmées à l'échelle Européenne mais semblent cohérentes au vu de l'épaisseur moindre des horizons organiques. Le robinier entraînerait donc bien un recyclage de la matière organique plus rapide que celui observé dans les parcelles dominées par des chênes natifs.

L'augmentation de la teneur en azote, et surtout en nitrate, semble favoriser le développement d'une couverture végétale plus importante dans le sous-bois (Figure 19). En Normandie, cette augmentation de la couverture ne semble pas liée à une biomasse accrue (Table 6)

suggérant une modification des traits à l'échelle de la communauté végétale. Une augmentation de la couverture de cette strate pourrait aussi être liée à un meilleur accès à la lumière favorisant la production de biomasse végétale (Fortier *et al.*, 2011). Les résultats obtenus à l'échelle du gradient ne montrant pas d'ouverture accrue de la canopée dans les parcelles où le robinier est présent (Figure 17), l'hypothèse de l'augmentation de la fertilité des sols est probablement à retenir. Contrairement à l'observation fréquente d'effet négatif sur la richesse spécifique et la diversité (p. ex. Benesperi *et al.*, 2012; Kou *et al.*, 2016) nos résultats ne montrent pas de différence entre parcelles dominées par le robinier faux-acacia et celles dominées par les chênes natifs (Figure 19). Une augmentation de la diversité (mais pas de la richesse spécifique) a en revanche été observée dans les parcelles où le robinier est mélangé au chêne natif. Différencier entre l'effet positif fréquemment observé du mélange d'essence sur les communautés végétales de sous-bois (Mölder *et al.*, 2008) et le fait qu'une de ces deux essences est exotique est complexe et aurait nécessité des parcelles de référence mixtes entre essences natives. Il parait néanmoins probable qu'il s'agisse principalement de l'effet de mélange, plus que l'effet de l'espèce exotique. A l'échelle de la Normandie, où les communautés végétales ont été étudiées avec plus de précision, il n'y a eu de favorisation de la présence d'espèces nitratophiles ou exotiques (Appendice C) mais ces résultats n'ont pas été, pour l'instant, confirmés à plus grande échelle. Comme indiqué dans le chapitre 3, l'augmentation observée de la teneur en nitrate reste relativement limitée en terme absolu, malgré l'augmentation relative aux parcelle natives et restent dans la gamme de variation observée ailleurs en Normandie pour des parcelles natives (Trap *et al.*, 2011).

Les répercussions de la présence du robinier sur la faune du sol restent relativement mal comprises mais suggèrent un faible impact du robinier faux-acacia sur ces organismes (p.ex. Brygadyrenko, 2015; Buchholz *et al.*, 2015; Della Rocca *et al.*, 2016). Il n'y a pas eu de changements dans l'abondance, la richesse spécifique ou la diversité des communautés de la macrofaune épigée (Brygadyrenko, 2015), des coléoptères saproxyliques (Della Rocca *et al.*, 2016) ou encore des carabes et araignées (Buchholz *et al.*, 2015). Seuls Degomez & Wagner (2001) ont observé une diminution de l'abondance et de la richesse spécifique pour des arthropodes épigés.

Les résultats présentés dans le chapitre 2 montrent une absence de réponse de la microfaune (nématodes) et mésofaune (collemboles et acariens) endogé à la présence du robinier l'échelle Européenne. Ces résultats sont surprenants au vue des changements importants observés dans les caractéristiques de la litière

Concernant cette première hypothèse générale relative au robinier faux-acacia il est donc possible de conclure :

- Qu'il y a bien des différences fonctionnelles importantes entre le robinier et les essences natives considérées ici (chêne sessile et châtaigner commun) en terme de traits foliaires et dans les associations symbiotiques réalisées avec la microflore.
- Que le robinier tend à altérer la fonction de recyclage de la matière organique, et la répartition des stocks d'azote, dans les écosystèmes forestiers. L'absence de prise en compte des variations intersaisonnière dans la cadre de ces travaux mitige en revanche la généralisation de ces résultats.
- Que les communautés végétales sont bien impactées par la présence du robinier, mais uniquement dans leur couverture et la prévalence de certains traits. La richesse spécifique et la diversité ne sont pas affectées par la dominance du robinier, mais peuvent l'être quand il est en mélange. Malgré l'augmentation de la teneur en nitrate, le robinier ne semble pas favoriser les espèces nitratophiles ou, inversement, défavoriser les espèces oligotrophes.
- Que les communautés animales de la mésofaune semblent peu affectées à grande échelle par la présence du robinier, mais peuvent l'être localement (p. ex. en Normandie) à la fois dans leur abondance et leur diversité. La macrofaune, étudiée seulement localement en Normandie, reste également relativement peu affectées malgré les autres modifications induites par le robinier.

**H2.1** : *L'impact du robinier varie le long d'un gradient latitudinal de par les différences de climat et d'essences natives dominantes.*

Les espèces exotiques, ayant donc pu être dispersées hors de leur aire de répartition naturelle, sont confrontées cette nouvelle zone à un second filtre, climatique cette fois, déterminant leur capacité à survivre localement (Figure 3). Le climat, et le type de biome envahit, déterminent également le taux d'envahissement et l'impact des invasions biologiques sur les écosystèmes (Schweiger *et al.*, 2010; Pyšek *et al.*, 2012; González-Moreno *et al.*, 2014; Martin *et al.*, 2017) avec une influence probablement forte des changements climatiques présents et futurs sur ces impacts (Dukes & Mooney, 1999; Davidson *et al.*, 2011) en affectant notamment les interactions biotiques (Schweiger *et al.*, 2010) et le recyclage des nutriments (Martin *et al.*, 2017).

Dans le cas du robinier faux-acacia il a été montré que sa distribution dans les zones où il est allochtone était fortement dépendante du climat, l'optimum de distribution allant de climats subméditerranéens à continentaux chauds (Sukopp & Wurzel, 2003; Cierjacks *et al.*, 2013; Li *et al.*, 2014). La température influence le taux de germination des graines et sa cinétique (Giuliani *et al.*, 2015), un déterminant important de l'invasion par le robinier (Masaka & Yamada, 2009). Les changements climatiques sont également susceptibles de modifier le potentiel envahissant du robinier (Kleinbauer *et al.*, 2010) ainsi que sa biomasse, production ,primaire, nodulation et teneur en azote et phosphate (Olesniewicz & Thomas, 1999). Les différences de climat actuelles sont également susceptibles d'influencer la densité du robinier (Kleinbauer *et al.*, 2010), et sa phénologie (Walkovszky, 1998) avec des répercussions probables sur le fonctionnement de l'écosystème (Pereira *et al.*, 2011; Medina-Villar *et al.*, 2015, 2016).

Les résultats présentés dans le Chapitre 2 montrent une influence forte de la latitude du site d'étude sur de nombreuses variables. La latitude implique ici de multiples facteurs différenciant les sites : climatiques, pédologiques et dans les espèces formant les communautés végétales et animales. Plus important encore pour la perception de l'impact du robinier, les essences natives dominantes utilisées comme contrôle différent entre régions considérées. Bien qu'appartenant toutes au genre *Quercus* (*Q. ilex* en Catalogne, *Q. pubescens* en Aquitaine, *Q. petraea* en Normandie et *Q. robur* en Wallonie) ces essences présentes des différences fonctionnelles importantes. Si une part importante de ces différences sont dans leurs préférences stationnelles, et donc liées aux différences climatiques et pédologiques entre régions, ces espèces diffèrent également dans leurs traits (p. ex. les feuilles coriaces du chêne vert). Dans la mesure où l'évaluation, ici, de l'impact du robinier est relative par

rapport au contrôle il est complexe ici de décorréler l'influence des différences de climat, pédologie et d'essence au sein de la « latitude ». Ces essences étant localement dominantes et associées au robinier cette méthodologie reste néanmoins pertinente pour appréhender l'impact du robinier à large échelle.(Perie & Ouimet, 2008)

Les variables relatives au substrat les plus influencées par la latitude sont la teneur en azote (total et minéral sous forme de nitrate) et en carbone totale, qui augmentent avec la latitude. En revanche, les biomasses microbiennes (en carbone) et fongiques (en ergostérol) ainsi que la masse volumique apparente diminuent avec la latitude. La teneur en azote et carbone totale accrue semble indiquer une augmentation de la quantité de matière organique dans les sites les plus au nord (appuyée par la diminution de la masse volumique apparente ; Perie & Ouimet, 2008). Elle semble liée à l'augmentation relative de l'épaisseur des horizons organiques. Néanmoins si les valeurs de teneur en carbone organique des horizons superficiels restent dans la gamme de variation théorique pour les sites les plus au sud (Catalogne et Aquitaine ; EEA, 2010) les valeurs des sites les plus au nord sont, elles, extrêmement faibles (environ trois fois inférieures aux valeurs théoriquement attendues) pour les parcelles natives comme exotiques (EEA, 2010).

Cette faible teneur en carbone organique, malgré l'augmentation de la teneur en carbone total, explique probablement la diminution importante de la biomasse microbienne et fongique avec la latitude. La teneur accrue en azote organique (surtout en nitrate mais également en ammonium) laisse suggérer une minéralisation plus intense de la matière organique dans les sites les plus au nord. L'activité de minéralisation étant fortement dépendante de l'humidité des sols (augmentant ici avec la latitude), et donc des précipitations (Bottner *et al.*, 2002; Rey *et al.*, 2008). Hélas, dans le cadre des travaux présentés ici, l'ammonification et la nitrification n'ont été mesurés qu'en Normandie et non le long du gradient ne permettant pas de confirmer cette observation. Une diminution de la richesse spécifique et de la diversité des communautés végétales de sous-bois a également été observée ainsi qu'une augmentation de l'abondance des acariens oribatidés.

Bien plus que les changements absolus liés à la latitude, et communs aux parcelles dominées par les essences natives ou par le robinier, l'intérêt est ici d'évaluer les différences dans l'impact du robinier entre les régions considérées. Ces changements sont relativement communs, mais ne semblent pas directement (c.-à-d. linéairement) liés aux changements de régime de précipitations ou de températures. Surtout, il s'agit principalement de différence dans l'intensité de l'impact, ou sa significativité, et non de changements dans la direction de l'impact. C'est le cas, par exemple de l'épaisseur des horizons organiques qui diminue en présence du robinier et à grande échelle mais n'est pas significative en Catalogne. Le ratio carbone sur azote du sol diminue également en présence du

robinier, mais n'est lui pas significatif en Wallonie. Un cas inverse est celui de l'azote en Normandie. Si la tendance générale est à l'augmentation de la teneur en azote total et en nitrate dans les sols (avec une influence positive de la latitude) cette augmentation n'est localement significative qu'en Normandie alors qu'elle est très faible en Wallonie. Les différences de climat entre les deux, et elles existent notamment en termes de températures extrêmes estivale et hivernale, ne semblent pas suffisante ici pour justifier une telle différence. De la même manière, la biomasse fongique tend à diminuer partout, mais diffère significativement uniquement en Catalogne. Ce cas semble plutôt illustrer des différences de traits entre espèces de chêne qu'un facteur climatique : les feuilles du chêne vert (*Q. ilex*) sont beaucoup plus coriaces que celles des autres essences, ce qui pourrait alors favoriser les champignons saprophages, plus à même de décomposer ces feuilles récalcitrantes. Si la latitude influence la richesse spécifique et la diversité des communautés végétales de sous-bois, elle ne semble pas influencer les différences relatives entre les communautés sous essences natives et sous le robinier. Cette observation s'applique également à la faune du sol.

A l'exception de la tendance observée au niveau de l'épaisseur des horizons organiques il semble donc que l'hypothèse d'impacts différents du robinier en fonction de la latitude, et donc des conditions climatiques et pédologiques, peut être rejetée. Le climat a bien une influence sur l'envahissement du robinier, comme démontré dans la littérature. Le climat influence également le fonctionnement de l'écosystème, et des communautés végétales, en présence du robinier. En revanche, les différences climatiques entre régions ne semble pas avoir d'influence majeur son impact au vu de son effet similaire sur les parcelles dominées par les essences natives.

**H2.2** : *L'effet du robinier va différer selon l'essence native utilisée comme contrôle natif, notamment de par les différences fonctionnelles entre essences natives.*

L'étude réalisée en 2016 en Normandie (Chapitre 3) avait pour objectif secondaire de tester cette hypothèse. Lors de cet échantillonnage deux essences natives localement dominantes ont été considérées : le chêne sessile (*Quercus petraea*) et le châtaigner commun (*Castanea sativa*) à la fois en peuplements monospécifiques et en mélange avec le robinier. Comme discuté précédemment ces deux essences diffèrent du robinier par leur teneur foliaire en azote ainsi que par leur capacité, ou incapacité, à réaliser des symbioses rhizobiennes (Figure 22). Ces essences diffèrent également entre elles. Le châtaigner occupe ainsi une position intermédiaire entre le robinier et le chêne en terme de teneur en carbone des feuilles, et de teneur en matière sèche. Là où le chêne diffère du robinier pour ces traits, le châtaigner n'est ni différent du chêne ni différent du robinier. L'hypothèse est donc que ces différences, et d'autres non quantifiées, sont susceptibles de modifier l'effet relatif du robinier sur les paramètres affectés.

Les résultats obtenus dans le cadre de l'échantillonnage de 2016 en Normandie, et présentés au chapitre 3 tendent à confirmer cette hypothèse pour une part importante des variables mesurées. L'ordination présentée en Figure 23, basée sur la couverture de la canopée et l'aire basale des trois essences, illustre assez clairement ces différences pour un ensemble de variables physico-chimiques et biologiques. Malgré l'effet relativement limité des différences d'essences on observe une différenciation, la plus importante entre parcelles dominées par les essences natives et celles dominées par le robinier en fonction du premier axe. Ces résultats reflètent ceux présentés précédemment. Il y a, en revanche, également une différenciation entre parcelles dominées par le chêne et celles dominées par le châtaignier, ou le robinier, en fonction du deuxième axe. Ces différences se retrouvent notamment dans l'épaisseur des horizons organiques, la couverture de la canopée et la biomasse fongique (concentration en ergostérol) qui sont plus importants sous le chêne que sous le châtaigner. Inversement, le châtaigner semble favoriser une masse volumique apparente plus élevée ainsi qu'une augmentation qu'une nitrification, et une teneur en nitrate, plus élevée.

Ces différences entre essences natives se retrouvent dans l'évaluation de l'impact du robinier, qui varie selon l'essence considérée comme contrôle pour de nombreuses variables. On peut ainsi voir que le robinier, seul ou en mélange, entraine une diminution de la masse volumique apparente (MVA) du sol par rapport au châtaigner, mais pas par rapport au chêne. Une MVA plus faible implique une

porosité plus importante du sol et/ou une teneur en matière organique plus élevée (Perie & Ouimet, 2008). Cette différence pourrait expliquer l'abondance plus élevée en collemboles, observée également sous le robinier par rapport aux parcelles dominées par le châtaigner. Inversement, l'abondance des acariens diminue sous le robinier, seul ou en mélange, mais uniquement par comparaison aux parcelles de chêne. On retrouve également des différences importantes dans l'impact du robinier, en fonction de l'essence native considérée, dans les variables liées au cycle de l'azote. La teneur totale du sol en azote n'augmente dans les parcelles de robinier que quand le chêne sessile est utilisé comme contrôle, et pas le châtaignier, causant également une diminution du ratio carbone sur azote. La teneur en azote est un trait foliaire pour lequel il y a une différence importante entre les trois essences : le robinier a la teneur la plus élevée, le chêne sessile la plus faible (Figure 22). Le châtaignier, en revanche, présente une teneur foliaire en azote intermédiaire entre celles des deux autres essences mais différente des deux. L'augmentation de la teneur en azote du sol là où le robinier est dominant provient donc probablement d'un apport différencié en azote selon les traits de la litière arrivant au sol.

Malgré cette augmentation de la teneur totale en azote, incluant donc la fraction organique, les répercussions sur les processus de minéralisation paraissent contre-intuitif. Une diminution drastique de l'ammonification peut être observée dans les parcelles où la teneur totale en azote augmente (ammonification qui diminue également fortement dans les parcelles mixtes, dont la teneur totale en azote ne diminue pas ; Figure 24). Si on observe une diminution de la teneur en ammonium en présence du robinier, c'est uniquement dans les parcelles de mélange avec le chêne, et non dans les parcelles où le robinier est dominant et où la teneur totale en azote diminue. De manière similaire, si on observe bien une augmentation de la teneur en nitrate dans les parcelles dominées par le robinier et appariées au chêne sessile, la tendance est à une diminution de la nitrification. Dans les deux cas, teneur en nitrate et nitrification, il n'y a pas de différence entre robinier et châtaigner. Ces divergences entre stocks et processus paraissent paradoxales si on exclut le facteur temporel. Comme démontré par Pereira *et al.* (2011) et Rice *et al.* (2004) il y a une variation saisonnière importante à la fois dans les stocks de nitrate, minéral ou organique, et la minéralisation de l'azote. Pour l'ammonification, Pereira *et al.* (2011) montrent que celle-ci est maximale en de juillet à septembre correspondant à la dégradation des fleurs du robinier, riches en azote et facilement dégradable (Medina-Villar *et al.*, 2015).

Sous les parcelles de robinier appariées au châtaigner, on observe une augmentation drastique du taux de décomposition de la litière (Figure 25), qui n'est pas observée dans les parcelles appariées au chêne. Ces résultats paraissent paradoxaux par rapport aux observations précédentes sur la qualité chimique de la litière (teneur en azote). Il s'agit ici du taux de décomposition agrégé de litières

d'essences différentes : le hêtre (*Fagus sylvatica*) et l'érable champêtre (*Acer campestre*). Les résultats obtenus montrent donc une activité de décomposition accrue dans ces parcelles, indépendamment de la provenance de la litière. S'il ne semble pas y avoir de changement dans la biomasse microbienne ou fongique, l'augmentation concomitante de la respiration potentielle du sol montre néanmoins une activité microbienne plus importante. Les communautés de la faune du sol sont également affectées dans ces parcelles (Table 6). On observe ainsi une diminution de la divergence et équitabilité fonctionnelle de la macrofaune, à savoir un resserrement des valeurs prises par les traits et une proportion moindre d'individus présentant les traits les plus éloignés de la moyenne communautaire. Les groupes de la macrofaune dont les traits ont été utilisés incluent une grande proportion d'organismes fragmenteurs au sein desquels on observe un diminution de la proportion de lombrics, au profit d'individus pourvus d'organes visuels occupant la litière. On observe également une augmentation importante de l'abondance des collemboles, qui participent également à la dégradation de la litière. Inversement, dans les parcelles appariées au chêne sessile et où le robinier est présent on observe une augmentation relative de la proportion de lombrics au sein de la macrofaune, et une diminution de l'abondance en acariens sans effet apparent sur le taux de dégradation de la litière.

La prise en compte de l'impact du robinier a rarement été faite par comparaison avec plusieurs espèces natives (Medina-Villar *et al.*, 2015; Della Rocca *et al.*, 2016). La plupart des études utilisent seulement un type de végétation native comme référence pour extrapoler l'impact (Von Holle *et al.*, 2006; Benesperi *et al.*, 2012; Medina-Villar *et al.*, 2016). Certains ont également étudié l'effet du mélange entre une essence native dominante et le robinier (Pereira *et al.*, 2011) ou considéré un mélange d'essence native comme référence (Rice *et al.*, 2004). Si l'argument biologique le justifie, c'est le cas en milieu forestier géré, il parait important de prendre en compte plusieurs essences natives, et mode de gestion, afin d'appréhender l'effet d'un arbre exotique sur le sous-bois.

### ***2.3. La renouée du japon : cas d'étude d'un mécanisme potentiel d'effet des invasions biologiques sur les réseaux trophiques du sol et son fonctionnement***

**H3** : *Les métabolites secondaires allélopathiques de la renouée du Japon ont un impact sur les communautés de la biocénose du sol et le réseau trophique décomposeur.*

La renouée du Japon (*Reynoutria japonica*) est une plante pérenne développant un dense réseau rhizomatique au sein du sol, surtout dans les horizons superficiels (Smith *et al.*, 2007). Ces rhizomes contiennent, produisent et libèrent de nombreux métabolites secondaires (Vastano *et al.*, 2000; Vaher & Koel, 2003) dont beaucoup sont allélopathiques et affectent les autres plantes (Gerber *et al.*, 2008; Aguilera *et al.*, 2010; Murrell *et al.*, 2011; Dommanget *et al.*, 2014) et la microflore (Daayf *et al.*, 1995; Chan, 2002; Filip *et al.*, 2003; Kumagai *et al.*, 2005; Hedenec *et al.*, 2014). L'effet de ces composés sur la faune du sol, et les réseaux trophiques souterrain, reste en revanche mystérieux (Skubala & Mierny, 2009). Quelques cas de toxicité directe de composés phénoliques sont documentés (p. ex. Isman & Duffey, 1982), ainsi que des cas d'effet répulsif sur les microarthropodes (Asplund *et al.*, 2015). Un effet indirect sur les microbivores par altération de la disponibilité de la ressource trophique microbienne parait également probable, et expliquerait en partie les observations sur le terrain (p. ex. Hedenec *et al.*, 2014; Tamura & Tharayil, 2014).

L'expérience dont les résultats sont présentés dans le Chapitre 4 vise à tester l'hypothèse d'un effet chimique de la renouée du Japon sur la faune du sol. Cet effet est quantifié grâce à l'utilisation de charbon actif permettant l'adsorption de molécules organiques dont les métabolites secondaires et donc d'inhiber l'effet allélopathique (Appendice D ; Ridenour & Callaway, 2001). En supprimant l'effet allélopathique il est alors possible de prendre partiellement en compte l'effet de l'addition de nutriments à la rhizosphère par la renouée du Japon. Les communautés microbiennes, de nématodes et de la mésofaune (acariens et collemboles) ont été étudiées avec cette méthodologie.

**H3.1** : *Les composés allélopathiques produits par les rhizomes de la renouée impactent négativement les microorganismes du sol. Cet impact se répercute négativement par cascade trophique aux niveaux supérieurs du réseau trophique.*

Contrairement à l'hypothèse de l'effet indirect par un impact sur les communautés microbiennes, ces organismes semblent peu affectés par l'allélopathie de la renouée (Chapitre 4). Le contraste avec les résultats de la littérature sur la biomasse microbienne peut-être lié à une concentration plus faible en métabolites secondaire par rapport aux études en laboratoires sur ces composés (Daayf *et al.*, 1995; Kumagai *et al.*, 2005) et/ou à l'absence des composés libérés *in situ* par la dégradation de la litière et lessivés dans le sol (Parepa *et al.*, 2012; Lavoie, 2017). Une absence de changement de la biomasse fongique est fréquemment observée sur le terrain les résultats observés ici sont donc cohérents (Lecerf *et al.*, 2007; Tamura & Tharayil, 2014).

En l'absence d'effet démontré sur les communautés microbiennes l'hypothèse de répercussions sur les microbivores, et le reste de la mésofaune du sol, par altération de la ressource trophique parait improbable. Néanmoins, les niveaux trophiques supérieurs (nématodes, mésofaune) sont malgré tout affectés par l'extrait de renouée du Japon. Concernant les communautés de nématodes, comprenant plusieurs groupes trophiques bien différenciés, on observe des changements (négatifs ou positifs) de l'abondance des bactérivores, fongivores et phytoparasites mais pas des prédateurs (Table 9). Sans études sur l'effet de la renouée du Japon sur les nématodes, ces résultats ne peuvent pas être mis en perspective. Ils suggèrent néanmoins qu'il y a bien une régulation trophique ascendante des niveaux inférieurs du réseau au vu des réponses différenciées par groupe trophique (Viketoft & van der Putten, 2015). La méthodologie d'échantillonnage utilisée ici, basée sur un unique prélèvement au terme de l'expérience, n'est pas à même d'appréhender l'aspect dynamique des interactions entre niveaux trophiques (Lurgi *et al.*, 2014; David *et al.*, 2017). La situation observée à la fin de l'échantillonnage pourrait alors refléter un décalage temporel dans la réponse de différents niveaux trophique. Les temps de génération de beaucoup d'organismes de la mésofaune sont relativement longs (p. ex. Prinzing *et al.*, 2002; Ermilov & Lochynska, 2008). En prenant l'exemple des acariens prédateurs, un mois n'est peut-être pas suffisant pour qu'une ressource trophique accrue ait un effet sur la démographie (c.à-d. modèles prédateurs-proie de Lotaka-Volterra).

La répercussion sur la structure du réseau trophique a été évalué en comparant les réseaux des communautés exposés, ou non, aux métabolites secondaires allélopathiques de la renouée. Les résultats montrent par calcul que l'effet allélopathique contribue à une altération des relations entre les différents niveaux trophiques du réseau. Plus particulièrement, l'inhibition de l'extrait de rhizome de renouée accroit l'interdépendance entre compartiments, ou taxons, du réseau trophique microbien. Ainsi, la corrélation positive entre la biomasse microbienne et l'abondance de ses consommateurs se renforce. On observe également un renforcement des liens prédateurs-proies entre collemboles et acariens gamasidés, ou des nématodes fongivores et prédateurs.

**H3.2** : *La libération de ces composés dans la rhizosphère constitue également un apport nutritif à la rhizosphère, cet apport mitigeant ou compensant les effets négatifs allélopathiques.*

Cette sous-hypothèse repose sur la distinction entre l'effet des métabolites secondaires allélopathiques de la renouée du Japons et de l'apport en nutriments solubles par les rhizomes. Cette distinction est rendue possible par l'utilisation du charbon actif, capable de retenir certaines molécules organiques comme les composés phénoliques (Ridenour & Callaway, 2001; Dąbrowski *et al.*, 2005) dont font partie certains métabolites secondaires de la renouée du Japon (p. ex. catéchine et resvératrol ; Vastano *et al.*, 2000; Vrchotová & Šerá, 2008; Fan *et al.*, 2010; Tucker Serniak, 2016). L'adsorption de ces composés permet de produire une solution aqueuse sans métabolites secondaires phénoliques (testé sur le *trans*-resvératrol ;

Le ratio entre le carbone de la biomasse microbienne et l'ergostérol de la biomasse fongique tend à répondre de manière positive à l'allélopathie (par diminution de la biomasse microbienne) et négative à l'ajout de nutriments (par augmentation de la biomasse microbienne ; Chapitre 4). L'effet

combiné est, lui, intermédiaire correspondant aux résultats contrastés *in situ* sur ce ratio (Tamura & Tharayil, 2014; Suseela *et al.*, 2016; Stefanowicz *et al.*, 2017). Sur le terrain également, c'est la biomasse microbienne qui est la plus affectée, plus que la biomasse fongique (Beerling, 1990; Hedenec *et al.*, 2014; Stefanowicz *et al.*, 2016). Dans le cas présenté ici c'est l'ajout de nutriments, plus que l'effet allélopathique, qui semble prépondérant. Les nématodes, séparés par groupe trophique, tendent à répondre de manière distincte à l'apport en nutriment et à l'allalélopathie sans pour autant que ces distinctions soient généralisables et montrent une compensation. Concernant la mésofaune du sol toutes les réponses à l'extrait de renouée du Japon, que ce soit par apport trophique ou effet allélopathique, sont positives et s'additionnent pour donner un effet combiné lui-même positif. On peut donc difficilement parler de compensation ici mais plutôt de synergie.

Il y a donc peu d'éléments permettant d'accréditer cette sous-hypothèse. Des réponses distinctes à l'apport en nutriments et à l'allélopathie des extraits de renouée du Japon sont bien observées. En revanche, ces différences semblent plutôt idiosyncratiques et varient par exemple de manière non linéaire en fonction de la concentration de l'extrait.

## 3. Conclusions et perspectives

La méta-analyse globale a permis de démontrer l'effet des invasions biologiques végétales sur certains groupes de la faune du sol, les consommateurs primaires, en fonction de la structure de l'habitat (ouvert ou fermé). Une comparaison expérimentale incluant plusieurs espèces exotiques envahissant différents types d'habitats distinct pourrait permettre d'élucider les mécanismes sous-jacents aux différences observées au sein des communautés de la faune du sol. Les invasions biologiques par la faune du sol sont elle-même relativement mal connues. Si quelques cas sont bien documentés, comme par exemple des lombrics Européens en Amérique du Nord (Hendrit, 2006), d'autres restent peu documentées et mériteraient d'être étudiés.

L'étude à large échelle sur le robinier faux-acacia a permis d'illustrer les différences qui peuvent exister dans la réponse des écosystèmes forestiers dans des régions distinctes le long d'un gradient latitudinal. Utiliser les traits fonctionnels des communautés végétales et animales pourrait permettre d'approfondir ces observations en caractérisant fonctionnellement les modifications induites par les invasions biologiques. Il serait également intéressant de prendre en compte quantitativement les différences climatiques entre régions (et de décomposer la part d'explication de l'impact liée aux différences climatiques de celle liées aux différences d'essences) afin de fournir une prévision de l'effet des changements climatiques sur l'impact du robinier faux-acacia.

L'étude sur le robinier faux-acacia en Normandie a permis de mieux comprendre l'effet du robinier faux-acacia sur les communautés animales et végétales ainsi que sur le fonctionnement des écosystèmes (p. ex. le cycle de l'azote). Des différences importantes ayant été observées dans l'impact du robinier selon l'essence native utilisée comme référence, montrant l'aspect contextuel de la perception de l'impact d'une espèce exotique envahissante. Une généralisation de la prise en compte de plusieurs modalités de références à d'autres espèces exotiques envahissantes permettrait de mieux comprendre l'impact des invasions biologiques végétales.

Une manipulation expérimentale en laboratoire a démontré l'impact des composés allélopathiques de la renouée du Japon sur une partie de la faune du sol. Cette étude a montré que certaines espèces exotiques envahissantes sont susceptibles d'influencer la faune, et les réseaux trophiques, du sol par leur métabolisme secondaire. Une caractérisation chimique détaillée de ces composés, et une étude approfondie de leurs effets propres, permettrait de mieux comprendre les mécanismes sous-jacents et de pouvoir généraliser ces résultats à d'autres espèces exotiques envahissantes.

Les travaux réalisés dans le cadre de cette thèse ont permis d'apporter de nouveaux éléments à la compréhension de l'impact des espèces exotiques envahissantes (EEE), et plus particulièrement du robinier faux-acacia et de la renouée du Japon, sur la faune du sol, la végétation native et leur substrat. L'un des points forts de ce travail est la prise en compte de différentes échelles spatiales : une méta-analyse à l'échelle globale (Chapitre 1), une étude à large-échelle le long d'un gradient latitudinal (Chapitre 2), une étude approfondie à l'échelle régionale (Chapitre 3) et une expérience en laboratoire sur un mécanisme expliquant l'impact d'une espèce exotique envahissante (Chapitre 4). Un second point fort de ces travaux est la prise en compte simultanée, pour le cas de l'effet du robinier faux-acacia dans les écosystèmes forestiers, des communautés végétales de sous-bois, de la faune du sol et de plusieurs processus écosystémiques. Cette approche incluant à la fois les compartiments aériens et souterrains de l'écosystème a permis de fournir une vision plus exhaustive de l'impact du robinier en incluant les interactions entre compartiments et taxons.

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# Appendices

Table des appendices

## Appendice A

# Shifts and linkages of functional diversity between above and belowground compartments along a flooding gradient

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## Abstract

Trait-based approaches have the potential to reveal general and predictive relationships between organisms and ecosystem functioning. However the mechanisms underlying the functional structure of communities are still unclear. Within terrestrial ecosystems several studies have shown that many ecological processes are controlled by the interacting above and belowground compartments. However, few studies have used traits to reveal functional relationships between plants and soil fauna. Mostly, research combining plants and soil fauna solely only used the traits of one assemblage in predictive studies. Above (plants) and belowground (Collembola) compartments were sampled over a flooding disturbance gradient in northern France along the Seine River. We assessed shifts and linkages within these functional assemblages. Functional, and taxonomic, diversity indices were computed for each assemblage as well as community co-assembly through trait-convergence vs. trait-divergence patterns. Species richness of both taxa followed the same bell-shaped pattern along the gradient while a similar significant pattern of functional richness was only observed for plants. Further analyses revealed a progressive shift from trait convergence to divergence as constraints intensity decreased for plants but not for Collembola. Instead our results highlighted that Collembola traits were mainly linked to variations in plant traits. This lead, within Collembola assemblages, to convergence of a subset of perception related traits. Using a trait-based approach, our study highlighted that functional relationships occur between above and belowground compartments. We underlined that plant communities functional composition plays a key role in structuring Collembola assemblages in addition to the role of abiotic variables. Our study clearly shows that functional diversity provides a new approach to link the above and belowground compartments and might, therefore, be further considered when studying ecological processes at the interface between both compartments.

*Keywords:* Collembola, biotic and abiotic filters, plant communities, trait-convergence & trait divergence, functional traits, null models, environmental gradient

## 1. Introduction

With the urgent need of a predictive ecology, focusing on traits rather than species identities has contributed to a better understanding of general relationships linking communities to environments regardless of their species compositions.(McGill *et al.*, 2006; Messier *et al.*, 2010). The analysis of trait distribution within and among communities has shed light on different filtering processes and constraints on community assembly along environmental gradients (Freschet *et al.*, 2011; Violle *et al.*, 2012). Competition and other biotic interactions are expected to lead to trait overdispersion, or divergence, within a community as coexistence is dependent on the limitation of similarities in resource use among species (MacArthur & Levins, 1967; Pillar *et al.*, 2009). Conversely, strong abiotic filters are expected to generate an underdispersed, or convergent, trait distribution by constraining the range of possible trait values (Cornwell *et al.*, 2006; Pillar *et al.*, 2009). Despite the recent advances in trait-based community ecology there are still debates regarding the relative importance of environmental filters especially at small scale where local dispersal (stochastic process) and biotic interactions (deterministic processes) may prevail over abiotic environmental constraints (Bell, 2005; Bernard-Verdier *et al.*, 2012; Widenfalk *et al.*, 2015).

Terrestrial ecosystems are composed of two interdependent compartments: above and belowground (Hooper *et al.*, 2000). We are increasingly learning that soil biota is closely related to aboveground plant communities (Scheu, 2001; Wardle *et al.*, 2004b). There is compelling evidence that soil biota is responsive to the quality and quantity of organic matter inputs as well as to changes in micro-environmental conditions associated with changes in plant diversity (Wardle *et al.*, 2004b). As a feedback, by degrading litter, the belowground compartment for example controls nutrients availability for plants (Bardgett & Chan 1999).

The relationship between functional traits and various environmental gradients has been extensively studied for plants (e.g. Cornwell & Ackerly 2009; Violle *et al.* 2011; Bernard-Verdier *et al.* 2012; Mason *et al.* 2012) but less for the soil fauna (e.g. Ribera *et al.* 2001; Lambeets *et al.* 2009; Hedde *et al.* 2012; Salmon & Ponge 2012; Salmon *et al.* 2014). Most research combining plants and soil fauna either used plant traits to explain faunal taxonomic composition or used vegetation structure and composition to explain changes in faunal traits (Gorman *et al.*, 2013; Podgaiski *et al.*, 2013). Few studies assessed relationships between two

trophic levels in relation to environmental gradients using a trait-based approach (Moretti & Legg, 2009; Frenette-Dussault *et al.*, 2013; Fournier *et al.*, 2015). These interactions between soil fauna and plants are central in regulating ecosystem processes such as soil respiration (Heemsbergen *et al.*, 2004; Coleman & Whitman, 2005) and litter mass loss (Heemsbergen *et al.*, 2004; Cornwell *et al.*, 2008) which are involved in global processes such as carbon cycling (Schlesinger & Andrews, 2000). As such understanding the nature of these relations is critical and warrants additional work to properly assess their functional relationship with the essential aboveground compartment that is vegetation.

In this paper we studied the functional relationship between Collembola and herbaceous plants along a riparian flooding gradient (Seine River, France). Collembola are generally abundant and diverse within faunal soil communities (Hopkin, 1997; Coleman *et al.*, 2004) and, as such, functionally important. Collembola are also sensitive to changes in abiotic variables (Makkonen *et al.*, 2011; Bokhorst *et al.*, 2012) and show close links with plant traits (Scheu *et al.*, 1999; Salamon *et al.*, 2004; Endlweber & Scheu, 2006). We thus hypothesized a strong relationship between above and belowground compartments and tested whether (1) the assembly (taxonomic and functional) of plant and Collembola are affected by the flooding gradient; (2) there are clear linkages between the traits of Collembola communities and plant traits; (3) traits of both compartments converge at high flooding intensity (abiotic filter) but diverge where this constraint is released (biotic filter).

## 2. Material and methods

### ***2.1. Study site***

The study area was located on the banks of the Seine River (France) around the town of Petiville (49.4611 N, 0.5883 E). Although the area is 20 km away from the estuary (English Channel), the tidal range is still between 3 m (neap tide) and 6 m (spring tide) due to the very flat slope on the last part of the river (Guézennec *et al.*, 1999). Thus, this riparian area offers a good opportunity to study periodic flooding caused by tides. The mean annual temperature ranged from 8 to 12°C, and the mean annual rainfall from 600 to 1000 mm.

The vegetation closest to the riverside was herbaceous and dominated by sedges (Cyperaceae: *Scirpus* sp. or *Eleocharis* sp.) generally followed by a monospecific reed bed (*Phalaris arundinacea* L. or *Phragmites australis* (Cav.) Trin. ex Steud.). Willow groves (*Salix* sp.) with a typical riparian transition

understory were present at intermediate distances from the riverside. Planted poplars (*Populus* sp.) characterized the community closest to the dike (about 150m from the river) protecting the floodplain from direct flooding. 30 sampling units were placed at the study site. These sampling units were located to cover the widest possible range of hydrological, pedological, topographical and floral conditions with a minimal distance of 20 m separating them. Each of these units was sampled for plants, Collembola and several abiotic variables.

### *2.2. Abiotic variables*

In order to quantify flood intensity between the different sampling units, we monitored volumetric water content for 3 months using field sensors (EC-5 soil moisture sensor, Decagon Devices) and data loggers (EM5B analog data logger, Decagon Devices). At each sampling unit, bulk of soil up to a depth of 10 cm were extracted and kept in plastic bags for transportation to the laboratory. Soil samples were air dried and sieved at 2 mm. The pH (H2O) was measured according to NF ISO 10390. Granulometry was assessed without sample decarbonatation for 3 fractions: clay, silt and sand (NF X 31-107). Limestone (CaCO3) content was measured using a Bernard calcimeter (NF ISO 10693). Total carbon and total nitrogen content were measured by elemental analysis (NF ISO 10694 & NF ISO 13878). A correction was made with limestone content to determine organic carbon content. Cobaltihexamine was used to assess exchangeable cations (K & Mg) (NF X 31-130). Total conductivity was assessed using a ratio of 1 mass unit for 5 volume units. Canopy openness was evaluated visually during vegetation sampling and used to assess understory light availability. These results were compiled in an abiotic variables matrix (**E**, 30 sampling units × 12 abiotic variables).

### *2.3. Vegetation*

Within each sampling unit a 2 x 2 m quadrat was randomly placed and subdivided into four 1 x 1 m sub-quadrats. Vascular plant species were identified within each quadrat in June 2011. The presence or absence of species within the four sub-quadrats were added and used to estimate the relative abundance within the main quadrat. Species with total abundance accounting for less than 5 % of total abundance were ignored for analysis (Cornelissen *et al.*, 2003). Trait data were obtained from the TRY Plant Trait Database (Kattge *et al.*, 2011). Individual datasets within the database are referenced in Appendix 1. Multiple traits were selected supposedly reflecting different potential plant responses to flooding such as nutrient acquisition (vegetative/generative reproduction; Pérez-Harguindeguy *et al.* 2013), litter decomposability (LNC, LDMC; Fortunel *et al.* 2009), submersion tolerance (specific leaf area (SLA); Voesenek *et al.* 2006; plant height, Grime's CSR strategies, Raunkier's life-forms), competitive ability (leaf area, plant height; Westoby *et al.* 2002), productivity

(SLA; Lavorel *et al.* 2007), population recovery speed (seed mass, CSR strategies; Violle *et al.* 2011) and salinity tolerance (Ellenberg's value for salt tolerance). The qualitative variables were split into dummy variables for analysis (Tab 1). Data were stored in two separate matrices: plant relative abundance ($\mathbf{W}_V$, 30 sampling units × 30 species) and plant traits ($\mathbf{B}_V$, 30 species × 21 traits).

*Table 1:*

| Traits | Code | Type | Values |
|---|---|---|---|
| *Leaf texture* | *LA* | Factor | mesomorphic (4), hygromorphic (3), hydromorphic (2), helomorphic (1) |
| *Raunkier's life-forms* | *HEL, GEO, PHA, THE, CHA* | Factor | helophytes (H), geophytes (G), phanerophytes (P), therophyte (T), chamaephyte (C) |
| *Species reproduction type* | *REPG* | Binary | generative (1) or not (0) |
| | *REPV* | Binary | vegetative (1) or not (0) |
| *Grime's plant strategies* | *C* | Binary | competitor (1) or not (0) |
| | *S* | Binary | stress tolerator (1) or not (0) |
| | *R* | Binary | ruderal (1) or not (0) |
| *Leaf area* | *LA* | Numerical | $mm^2$ |
| *Specific leaf area* | *SLA* | Numerical | $mm^2$/ mg |
| *Leaf nitrogen content* | *LNC* | Numerical | % per leaf dry mass |
| *Leaf dry matter content* | *LDMC* | Numerical | mg (dry mass) / g (wet mass) |
| *Plant vegetative height* | *PLH* | Numerical | cm |
| *Seed dry mass* | *SDM* | Numerical | g / 1000 seeds |
| *Ellenberg's value for salt tolerance* | *ELL* | Integer | 0 (absent from saline sites) to 9 (species of extremely saline conditions) |

### 2.4. Soil collembola

Soil collembola were sampled twice in May and July 2011 at each sampling unit by taking a soil core (diameter: 5 cm, depth: 10 cm) using a steal corer and were stored in plastic bags and cool boxes for transportation to the laboratory. Collembola were then extracted for 15 days by the dry-funnel method before being counted and identified under a dissection microscope at the species level following several keys (Gisin 1960, Hopkin 2007). Data for both sampling dates were averaged in a single matrix. Trait data were obtained from the COLTRAIT database (Salmon & Ponge, 2012; Salmon *et al.*, 2014). Selected traits were representative of dispersion capacity (leg length relative to body length, furca length, pigmentation), defence mechanisms (number of pseudocells; Hopkin 2007) and resource management (presence of vision organs, number of ocelli, number of post-antennal organ (PAO) lobes). Unordered qualitative variables were split into dummy variables for analyses (Tab 2). Data were stored in two separate matrices: Collembola relative abundance ($\mathbf{W_C}$, 30 sampling units × 21 species) and Collembola traits ($\mathbf{B}_C$, 21 species × 11 traits).

*Table 2:*

| Traits | Code | Type | Values |
|---|---|---|---|
| *Shape* | *CYL, THK, GLO* | Factor | cylindrical, thickset, globular |
| *Furca length* | *LFU* | Ordered factor | long (4), average (3), reduced (2), rudimentary (1), absent (0) |
| *Scales* | *SCA* | Binary | present (1), absent (0) |
| *Pigmentation* | *PIGM* | Binary | present (1), absent (0) |
| *Visual organs* | *VIS* | Binary | present (1), absent (0) |
| *Post-antennal organs* | *PAO* | Binary | present (1), absent (0) |
| *Antenna length relative to head diagonal length* | *LANT* | Numerical | ratio |
| *Leg length relative to body length* | *LLBC* | Numerical | ratio |
| *Body length* | *LEN* | Numerical | millimetres (mm) |
| *Number of post-antenal organs lobes* | *LPAO* | Integer | |
| *Mean number of pseudocellula* | *PSTO* | Integer | |
| *Number of ocelli* | *OCE* | Integer | |

## 2.5. Data analysis

### *2.5.1. Abiotic gradient analysis*

Regular tidal flooding has a variety of effects on soil properties (*i.e.* regular waterlogging and drainage, concentration of various elements, soil texture, etc.). In order to characterize the gradient and positioning our sampling units along a single axis we performed a principal components analysis (PCA) on matrix **E** (Fig 1). The first two components accounted for 81% of data variability (50.1 % and 30.9 % respectively). Flooding intensity was strongly correlated to the first axis (94 %) making the first component representative of flooding-induced changes. Other abiotic variables were also strongly correlated with this axis such as soil pH, soil organic matter and soil total nitrogen. We used the sampling units scores on the first component of the PCA as a synthetic variable incorporating multiple abiotic variables and representative of a flooding gradient. Thereafter, in this study, we will use the term "flooding gradient", in reference to this synthetic abiotic variable (Axis 1 of PCA).

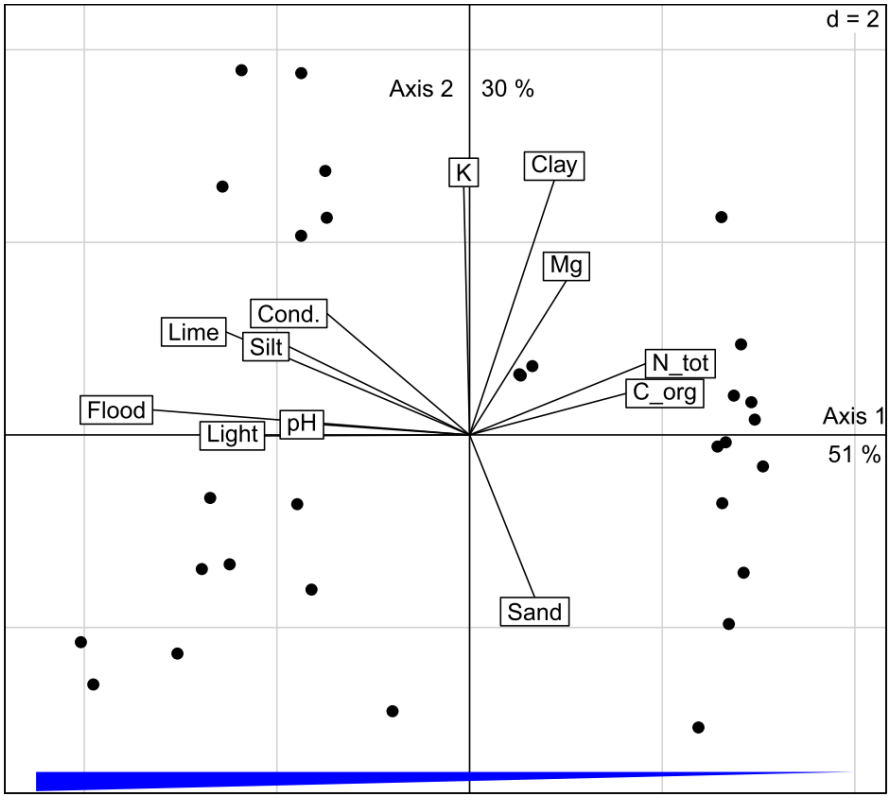


*Figure 1: Principal component analysis (PCA) ordination diagram of plots based on soil abiotic parameters. Points are sampling units. C, N, K, Mg: carbon, nitrogen, potassium and magnesium content. Silt, Clay, Sand: soil granulometry, pH: pH H2O, Light: canopy openness proportion, Lime: CaCO3 content, Cond.: conductivity and Flood: proportion of time with satu- rated water content. The blue polygon is used to represent the flooding gradient in other figures*

### *2.5.2. Functional and taxonomic patterns*

Species richness (Ric) was calculated for plants and Collembola at each sampling point. Functional diversity was assessed separately for plants and Collembola using the three complementary indices of Villéger *et al.* (2008): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). Prior to the calculation of indices we performed a principal coordinates analysis (PCoA) on a corrected species by species distance matrix with possible dimensionality reduction. FRic was then computed by finding the minimum convex hull volume that includes all species coordinates and therefore represents the volume occupied by a given community in the functional space. FEve measures the regularity of the distribution of abundance in functional space. FDiv is defined by the degree of maximization of dissimilarities between functional species and their abundance in functional space. These indices were calculated using the 'FD' R package (Laliberté *et al.*, 2014). We attempted to relate these indices to the flooding gradient using generalized linear models (GLM). Diversity indices were log-transformed to meet the assumption of normality when required. Details on model selection for each index as well as the coefficients of significant regressions are provided in appendix 2. All statistical analyses were performed using R software version 3.1.3 (R Core Team 2015). The significant level for all analyses was $p < 0.05$.

### *2.5.3. Trait-convergence and divergence*

Trait-convergence and divergence patterns were assessed using the "TCAP/TDAP" method proposed by Pillar *et al.* (2009). A trait-convergence assembly pattern (TCAP) can be identified when sites nearby on an ecological gradient consistently contain species with similar traits. Conversely, a trait-divergence assembly pattern (TDAP) can be observed when the turnover in trait-based community components is related to the gradient but with communities containing species with dissimilar traits. The analysis involves the use of three matrices: trait matrix **B** (i.e. $\mathbf{B}_V$ or $\mathbf{B}_C$), relative abundance matrix **W** (i.e. $\mathbf{W}_V$ or $\mathbf{W}_C$) and environmental matrix **E**. In order to assess trait-convergence along the flooding gradient trait-based data first need to be scaled up to the community level which was done by matrix multiplication defining $\mathbf{T} = \mathbf{B} \times \mathbf{W}$ (i.e. Community Weighted Means). Two distance matrices are defined: $\mathbf{D}_T$ and $\mathbf{D}_E$ using **T** and **E** respectively. Matrix correlation $\rho(\mathbf{TE}) = \rho(\mathbf{D}_T;\mathbf{D}_E)$, analogous to a Mantel test, is used to evaluate how TCAP in **T** is associated to ecological gradients in **E**. Trait-divergence assessment first involves a fuzzy clustering of species into types according to their traits resulting in matrix **U**. By matrix multiplication, $\mathbf{X} = \mathbf{U} \times \mathbf{W}$ will contain the composition of the community in terms of these types. Matrix **X** expresses both TCAP and TDAP (Pillar *et al.*, 2009). For relating **X** to **E** the distance matrices $\mathbf{D}_X$ and $\mathbf{D}_T$ are defined and matrix correlation used so that $\rho(\mathbf{XE}) = \rho(\mathbf{D}_X;\mathbf{D}_E)$. The trait-convergence component $\rho(\mathbf{TE})$ of $\rho(\mathbf{XE})$ is removed by computation of the partial

matrix (Mantel) correlation ρ(**XE.T**) which measures the level of congruence between TDAP and **E**. All matrix correlations were tested against null models defined according to the correlation being tested (see Pillar *et al.* 2009 for details). An iterative process is then used aiming at finding an optimal subset of traits that maximizes convergence, divergence or both (see Pillar & Sosinski Jr. 2003 for details). We initially assessed TCAP and TDAP within plants and Collembola communities in relation to the environmental variables. In addition we used plants community weighted trait means (CWM) as an environmental matrix in order to assess plants-induced trait-convergence or trait-divergence within Collembola communities. All TCAP and TDAP computations were performed using the 'SYNCSA' R package (Debastiani & Pillar, 2012).

While the TCAP/TDAP approach gives information on the nature of the patterns structuring community assemblages it does not reveal the position of those patterns along the flooding gradient. In that regard we computed mean pairwise distances (MPD) within communities ($\mathbf{W}_V$ or $\mathbf{W}_C$) based on species traits (pairwise functional distances matrix $\mathbf{D}_B$ defined by calculating Gower's distances on matrix **B**). These MPDs were assessed for non-random patterns by testing against a null-model. This model involved random permutations of taxa labels within the pairwise distances matrix maintaining data structure with randomized MPDs. Differences between observed MPDs and random MPDs were used to identify either convergence or divergence for each community along the flooding gradient. We initially tested plants and Collembola communities against the null model using all their traits. Subsets of traits previously found to maximize convergence (TCAP), divergence (TDAP) or both were then used to test for non-randomness within the communities. A generalized linear model (GLM) was fitted on the data with the flooding gradient as the explanatory variable. All MPD computations were done using the 'picante' R package (Kembel *et al.*, 2010) initially designed for use with phylogenic distances.

# 3. Results

## 3.1. Diversity patterns

The relationship between taxonomic richness and flooding gradient (Axis 1 of the PCA) demonstrated that plant ($R^2$ = 0.657, p < 0.001, n = 30; Fig. 2A) and Collembola ($R^2$ = 0.555, p < 0.01, n = 27 ; Fig. 2A) species richness showed a unimodal response to disturbance intensity. Plant functional richness showed a unimodal response to disturbance intensity (quadratic relationships: $R^2$ = 0.312, p < 0.05, n = 24; Fig. 2B) which was not observed for Collembola (Functional richness: $R^2$ = 0.172, p = 0.256, n = 24, Fig. 2B). Plant functional evenness did not match any known probability distribution and could not be regressed. Collembola functional evenness was successfully modelled in response to the flooding gradient but no significant pattern could be found ($R^2$ = 0.042, p = 0.460, n = 24, Fig. 2C). No model was able to explain plant or Collembola functional divergence along the flooding gradient ($R^2$ = 0.033, p = 0.403, n = 24 and $R^2$ = 0.031, p = 0.398, n = 24, respectively).

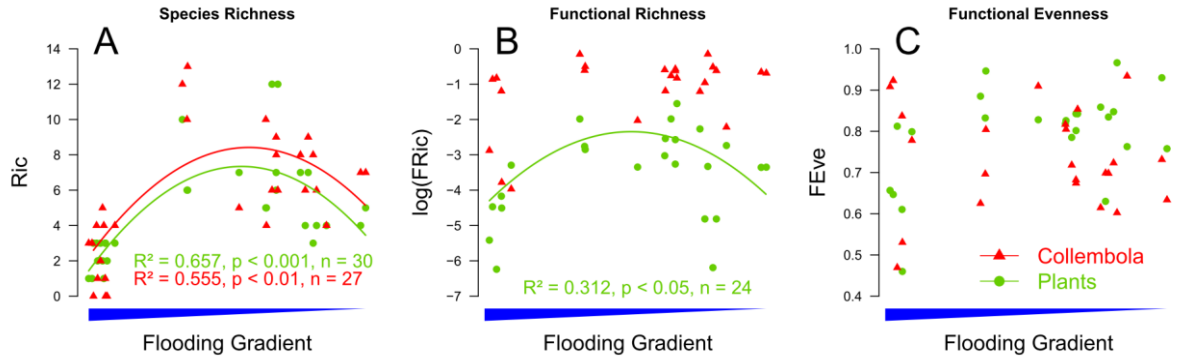


*Figure 2: Taxonomic and functional richness and evenness of vegetation (green points and line) and Collembola (red points and lines). (a) Taxonomic richness (Ric); (b) functional richness (FRic); (c) functional evenness (FEve). The flooding gradient explanatory variable is a synthetic index extracted from the PCA scores of sampling units on the principal component. $R^2$ values were not shown when not signifi- cant.*

### 3.2. Trait convergence and divergence assembly patterns

The flooding gradient induced maximum convergence ($\varrho$ = 0.666, $p$ = 0.002, Tab 3) in a subset of plant traits containing leaf nitrogen content (LNC), mesotrophic leaf texture (LTM) and a ruderal strategy (R). The same subset of traits with the addition of leaf dry matter content (LDMC) also maximised both convergence and divergence ($\varrho$ = 0.668, $p$ = 0.001, Tab 3). Maximum divergence ($\varrho$ = 0.630, $p$ = 0.001, Tab 3) was detected for a subset of traits composed of LNC, LDMC, R and vegetative reproduction (REPV). No subset of collembolan traits was found to maximise either convergence or divergence using the flooding gradient as explanatory factor (Tab 3). However, the use of plant functional traits (Community Weighted Means, matrix **T**) as an explanatory variable led to significantly maximised convergence ($\varrho$ = 0.467, $p$ = 0.025) of a subset of collembolan traits: legs length relative to body length (LLBL), number of PAO lobes (LPAO) and a globular or cylindrical shape (GLO or CYL).

*Table 3: Trait convergence and divergence assembly patterns for vegetation and collembolas using Pillar index (Pillar et al, 2009)*

| Explained matrix | Explanatory matrix | TCAP | | TDAP | | TCAP/TDAP | |
|---|---|---|---|---|---|---|---|
| | | ro | *p* | ro | *p* | ro | *p* |
| Vegetation | Environnement | *LA LNC LTM THE* | | *LNC ELL* | | *LA LNC LTM THE* | |
| | | **0,735** | 0,001 | **0,646** | 0,001 | **0,741** | 0,001 |
| Collembola | Environnement | *SCA PSTO* | | *PIGM PSTO* | | *VIS PSTO* | |
| | | **0,354** | 0,108 | **0,192** | 0,330 | **0,078** | 0,324 |
| Collembola | Vegetation community weighted means | *PAO LLBL LPAO OCE* | | *PIGM VIS LANT THK* | | *PIGM LANT* | |
| | | **0,618** | 0,008 | **0,587** | 0,121 | ***0,588*** | 0,052 |
| Collembola | Vegetation functional diversity indices | *PAO LLBL* | | *LFU LANT PAO THK* | | *OCE GLO* | |
| | | **0,547** | 0,009 | **0,576** | 0,009 | **0,570** | 0,005 |

Subsets of traits that maximise Trait Convergence Assembly Patterns (TCAP), Trait Divergence Assembly Patterns (TDAP) or both (TCAP/TDAP) are given in italic. See Tab 1 and 2 for details on traits. Values in bold are the result of a correlation test between community traits values and ecological variables. Values in black indicate significant result ($p$ < 0.05) while values in grey indicate non-significant results ($p$ >= 0.05).

### 3.3. Functional mean pairwise distance within plots

Differences between observed and null functional mean pairwise distances within plant communities showed no significant relationship with the flooding gradient when using all traits (quadratic relationship: $R^2 = 0.30$, $p = 0.146$, $n = 27$, Fig. 3). When using plant traits maximising both trait convergence and divergence along the gradient (LA, LNC, LTM and R, see Tables 1 & 3) we demonstrated a significant positive relationship with the flooding gradient (linear relationship: $R^2 = 0.75$, $p < 0.0001$, $n = 27$, Fig. 3). Similarly, using all Collembola traits in relation to the gradient we did not detect any apparent pattern (linear relationship: $R^2 = 0.163$, $p = 0.437$, $n = 25$) and no significant difference from 0 (*i.e.* random expectations; $V = 191$, $p = 0.458$, Fig. 4) suggesting an absence of trait convergence or divergence. When using the Collembola subset of traits maximising trait convergence and divergence (i.e. LLBL, LPAO, CYL and GLO, see Tab 2 & 3) in relation to variations in plant traits Community Weighted Means (matrix **T**), we demonstrated a significant difference from 0 ($V = 37$, $p < 0.001$) indicating lower than expected mean pairwise distances, i.e. trait convergence.

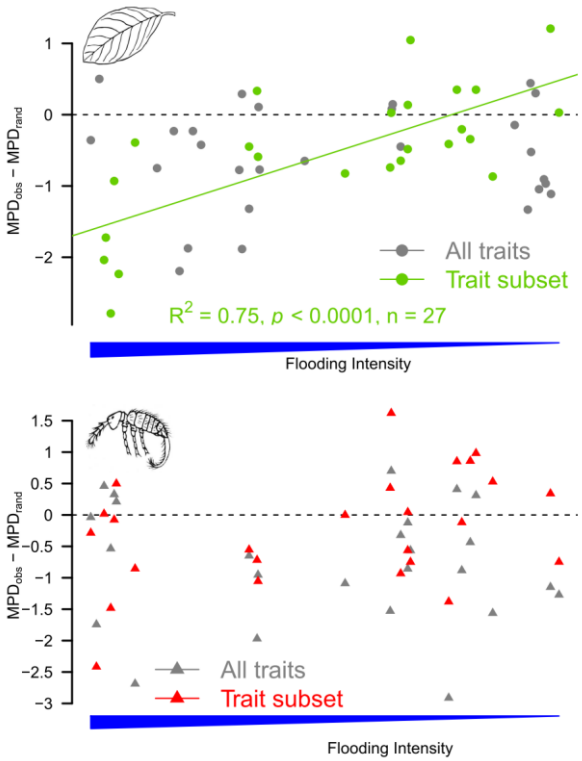


*Figure 3: Differences between observed and null functional mean pairwise distances (MPD) within plant (points) and Collembolan (triangles) communities along the gradient. Grey: distances calcu- lated using all traits; green/red: distances calculated using the trait subset determined to maximize convergence and divergence in veg- etation traits along the gradient (LNC, LDMC, LTM and R, see Tables 1 and 3). Dashed line represents the limit between a con- vergent and divergent pattern. Solid lines are significant regres- sions for the corresponding data. $R^2$ values were not shown when not significant*

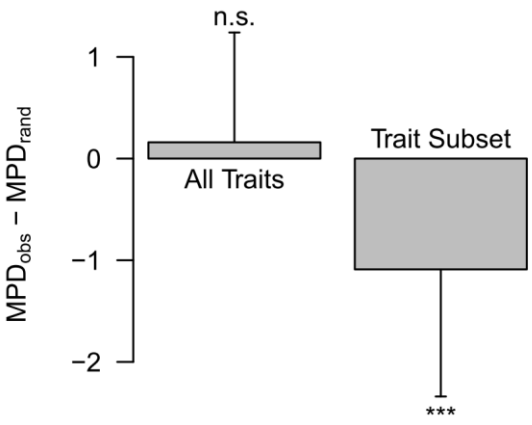


*Figure 4: Differences between observed (MPD.obs) and random (MPD.rand) mean pairwise distances (MPD) within Collem- bola communities. All traits: distances calculated using all Collembolan traits; trait subset: distances calculated using the trait subset determined to maximize convergence in Collembola traits in relation to the community-weighted mean of vegetation traits (LLBL, LPAO, PIGM & GLO, see Tables 2 and 3). Asterisks indicate significant differences after a Wilcoxon one-sample test between observed values and 0 (n.s.: P > 0,05, ***P < 0001).*

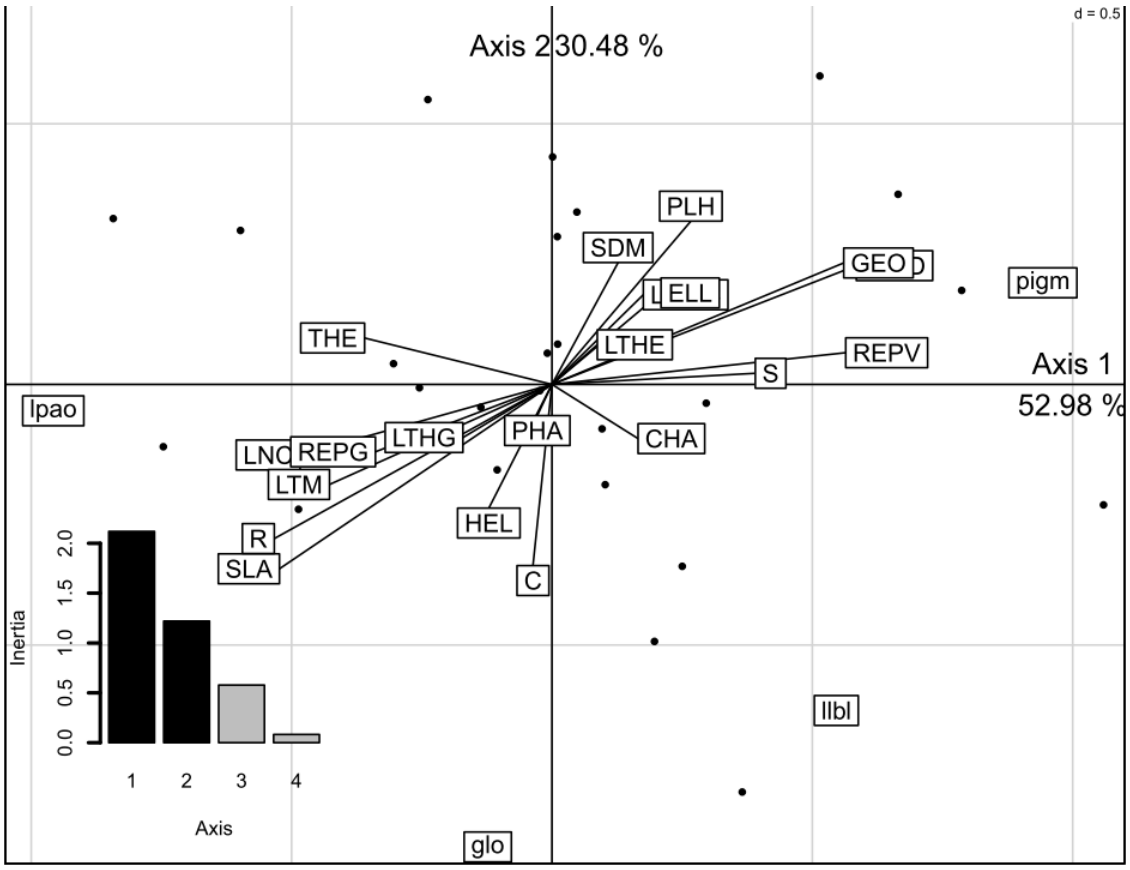


*Figure 2: Principal component analysis (PCA) of community-weighted Collembola traits exhibiting a trait-convergence assembly pattern (TCAP): 'pigm', 'llbl', 'glo' and 'lpao'. Community-weighted plant traits (in uppercase) were added as supplementary, or explanatory variables.*

# 4. Discussion

## *4.1. Above and belowground diversities along the gradient*

One of our aims was to assess the relationship between plant and Collembola taxonomic, and functional, diversity along a flooding gradient. A common response pattern between taxa was only revealed for taxonomic richness with a concave-down function. Other studies have already reported such a pattern along different flooding gradients either for plants (Lite *et al.*, 2005; Violle *et al.*, 2011) or for soil arthropods/Collembola (Lambeets *et al.*, 2009). This pattern matches the "intermediate disturbance hypothesis" of Connell (1978) which states that diversity of competing species is expected to be maximized at intermediate frequencies and/or intensities of constraints (but see Fox 2013). Diversity is supposedly limited for high and low disturbance (or stress) level due to two contrasting phenomenon: abiotic environmental filtering and interspecific interactions, respectively. The first limits the number of species able to colonize and survive under harsh environmental conditions while the second constrains species richness through, mostly, competitive exclusion (Wilson, 2007).

Contrary to our expectations, Collembola functional diversity (i.e. all three indices) as well as plant functional evenness and divergence were not found to be directly related to the flooding gradient but instead remained very stable. Patterns of stable functional diversity in relation to varying species richness have been observed for other taxonomic groups such as bats (Stevens *et al.*, 2003) and explained by functional redundancy between species. Only plant functional richness responded to the flooding gradient with the same concave-down pattern as observed for taxonomic richness. This relation between taxonomic and functional diversity has been previously documented for plants (Villéger *et al.*, 2008; Biswas & Mallik, 2010; Violle *et al.*, 2011). In our case, species richness significantly explained 77% of the functional richness for plants, which is in the range of previous studies: 62 % in Violle *et al.* (2011) and 87% in Villéger *et al.* (2008). Collembola functional richness was also correlated but slightly significantly (56%) to Collembola species richness. While this relationship for soil fauna was not assessed in the literature, Fournier *et al.* (2012) investigating earthworms in restored floodplains identified congruent patterns of species richness and functional trait diversity but Gerisch *et al.* (2012) investigating the response of ground beetles to flood disturbance, found an opposite pattern of taxonomic species richness and functional diversity. They concluded that flooding disturbance increased the number of species but that species were functionally redundant. The discrepancy between taxonomic and functional patterns for soil fauna could also be explained by stochastic movements of soil fauna communities (in our case Collembola) along the gradient governed by water runoffs or tides, in contrary to plants anchored in the soil. Lastly, we cannot exclude that the

lack of functionality of the considered faunal traits (especially the lack of ecophysiological traits) in relation to flooding may obviate for detecting strong relationship between species richness and functional richness.

### 4.2. Trait patterns and drivers within community assemblages

Having evaluated for the existence of patterns of functional diversity along the flooding gradient, we then assessed the relative importance of trait-convergence and divergence in relation to the abiotic variables characterizing the gradient. We demonstrated that environmental variations led to consistent trait-convergence and trait-divergence within aboveground communities suggesting that both abiotic and biotic filters structure plant communities.

Regarding plant traits, a subset of traits known to have a strong influence on litter decomposability (LNC, LDMC; Fortunel *et al.* 2009), resistance to disturbance (R strategy; Grime 2001) as well as competitive interactions and resource prospection (REPV; Pérez-Harguindeguy *et al.* 2013) was found to maximize trait-divergence. Trait-convergence was maximized for a subset including LNC, R and moisture preference (LTM). Analysis of mean pairwise distances (MPDs) enabled us to reveal the relative dominance of the two assembly patterns (i.e. TCAP and TDAP) along the gradient. Trait-convergence prevailed when flooding intensity was maximal (Fig. 3). As constraints decreased the assembly pattern shifts to trait-divergence with MPDs increasing drastically. This progressive shift could be explained by the intermediate disturbance hypothesis and by our considered abiotic variables. Violle *et al.* (2011) also used plant community traits to disentangle effects of abiotic and biotic filters in the regulation of species richness using a limited number of plant functional traits (SLA, height and Seed Mass). Similarly to our general findings, they demonstrated that SLA, increasing with flooding, controlled the species distribution through habitat filtering. On the other hand, species interactions (i.e. biotic filter) which were captured by community Height values played a strong consistent role throughout the disturbance gradient by reducing local species richness.

Regarding Collembola, the TCAP/TDAP approach allowed us to demonstrate that only plant functional traits and not abiotic filters explains their functional trait patterns. This result emphasizes the determinant role of plant characteristics and function for Collembola communities. However, while the considered environmental variables were found to be suitable to explain plant functional diversity other soil properties could have proven to have more impact on Collembola. Variables such as soil organic matter (Hasegawa, 2002), the volume of habitable pore space as well as the connectivity of those pores are known to impact Collembola community structure (Joosse, 1981; Didden, 1987). Nevertheless, previous studies have also demonstrated a stronger impact of plant functional

composition compared to environmental variables on soil fauna (soil quality: Gorman *et al.* 2013) and other arthropods (aridity gradient: Frenette-Dussault *et al.* 2013; land-use: Pakeman & Stockan 2014). Podgaiski *et al.* (2013) also found a stronger influence of plant functional diversity on spider traits (morphological or related to feeding behaviour) compared to the influence of burned and unburned plots supporting the habitat heterogeneity hypothesis. Influence of plants on Collembola is not solely related to habitat, even if differences in the diversity and quality of the plant litter are impacting predominantly many surface-living Collembola, as litter constitutes their main habitat (Hopkin 1997; Salamon *et al.* 2004). For example, a growing root system (Tilman *et al.* 2002) may increase the diversity of food resources (e.g. rhizospheric microorganisms) and also affect abiotic conditions such as water and nutrients (Hooper and Vitousek 1998; Niklaus *et al.* 2001) for soil-dwelling Collembola (Finlay 1985). For the first time we clearly linked aboveground plant traits and Collembola traits, even if previous studies showed that collembolan life forms (groups based on traits; Gisin 1943) were influenced by changes within the vegetation (Salamon *et al.* 2004; Chauvat *et al.* 2011; Salamon *et al.* 2011; Eisenhauer *et al.* 2011, Perez *et al.* 2013) indirectly suggesting a response of several Collembola traits to plant traits. It is worth noting that we were only able to use epigeous plant traits while endogenous traits could have proven to be more appropriate. However, several studies have demonstrated a correlation between leaf traits and their root counterpart (e.g. Craine *et al.* 2001) making them a valid proxy.

A significant trait-convergence assembly pattern was identified for a subset of morphological (LLBL, GLO) and vision-related Collembola traits (PAO, LPAO; Tab 3). In addition, and contrary to plants that are anchored in the soil, Collembola have several behavioural mechanisms at their disposal in order to escape flooding. One such mechanism is passive drifting which has been documented for the *Protaphorura* genus (Marx *et al.*, 2009) in flooded riparian areas. In addition, Collembola have been observed climbing on vertical surfaces in order to avoid the rising tide (Chauvat, *personal observation*). Such mechanisms could reduce the need for morphological adaptations to flooding disturbance and therefore limit the potential response of Collembola to flooding when only morphological traits are used. Such adaptations could explain a lack of a strong response of Collembola in our study, the considered morphological traits being only weakly filtered by abiotic variables. As such, more research on Collembola and soil fauna traits is required with more focus on physiological and behavioral traits.

Finally, other biotic variables are known to strongly influence Collembola communities such as fungal community composition (A'Bear *et al.*, 2014). Thus we suggest for future research linking Collembola (or soil fauna) and plant communities to integrate such microstructural soil variables. Especially as Collembola traits have been shown to vary with humus forms that are linked to soil organic matter (Salmon *et al.*, 2014). Nevertheless, in this study multiple Collembola trait subsets

showed a clear response pattern to variations in plant traits proving to be functional in relation to environmental biotic variables.

## 5. Conclusion

Functional diversity provides a new approach to link the above and belowground compartments. Using this approach we demonstrated that there was a strong linkage between plant and Collembola functional traits. We also underlined that plant functional diversity plays a key role in functional assemblages of Collembola in addition to the role of abiotic variables. While biodiversity declines in most ecosystems worldwide it becomes urgent to fully understand how aboveground changes are related to changes in the belowground and their effect on ecosystem functions. Such understanding and quantification would enable better prediction of future changes and provide a mean for proper management of ecosystems. In that regard, future studies should further explore multi-taxa functional traits variations in relation to environmental variables which provide valuable insights on community assembly rules and ecosystem function. In addition, experimental studies assessing the relevance and sensitivity of functional traits (selected on the base of TCAP and TDAP analysis) would be particularly useful in order to better understand those ecological mechanisms. To this aim, Collembola traits would need to be functional, behavioural and physiological rather than morphological only.

## 6. Acknowledgments

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## Appendice B

*Table 1 : Synthesis of invasive plant species effects on abundance of various soil and litter fauna taxa. Effect of IAS are based on a qualitative review of the considered paper, when stated or shown by the authors. Open habitats are grasslands, wetlands, moors and other habitats devoid of trees. Closed habitats are dense schrubs and forests. Cases highlighted (in bold) were included in the meta-analysis.*

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| *Acari* (total) | Positive | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | Open | Soil | *Buddleja davidii* | (Peltzer *et al.*, 2009) |
| | | **Open** | **Litter** | ***Phragmites australis*** | (Gratton & Denno, 2005) |
| | | Closed | Both | *Fallopia sachalinensis* | (Skubala & Mierny, 2009) |
| **No trophic group assigned** | | **Closed** | **Soil** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | | Closed | Soil | *Mikania micrantha* | (Guo-ming *et al.*, 2011) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Lindsay & French, 2006) |
| | | **Closed** | **Litter** | ***Lonicera maackiii*** | (Christopher & Cameron, 2008) |
| | | **Closed** | **Litter** | ***Microstegium vimineum*** | (McGrath & Binkley, 2009) |
| | | **Closed** | **Litter** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Standish, 2004) |
| | Neutral | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap & Phillips, 2001) |
| | | **Open** | **Soil** | ***Senecio jacobea*** | (Wardle *et al.*, 1995) |
| | | **Open** | **Litter** | ***Andropogon gerardii*** ***Schizachyrium scoparium*** | (St. John *et al.*, 2006) |
| | | Closed | Both | *Arundo donax* | (Maceda-Veiga *et al.*, 2016) |
| | | **Closed** | **Soil** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | **Closed** | **Soil** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| | | **Closed** | **Litter** | **Multiple (litter)** | (Tuttle *et al.*, 2009) |
| | Negative | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| | | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Open** | **Litter** | **3 invasive grasses** | (Wolkovich *et al.*, 2009) |
| | | Closed | Both | *Fallopia sachalinensis* | (Skubala & Mierny, 2009) |
| | | **Closed** | **Soil** | ***Ailanthus altissima*** | (Lindsay & French, 2006) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| | | **Closed** | **Litter** | ***Asparagus scandens*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Chrysanthemoides monilifera*** | (Lindsay & French, 2006) |
| | | **Closed** | **Litter** | ***Hedychium gardnerianum*** | (Bassett, 2014) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| *Acari* (Mesostigmata) | Negative | **Open** | **Soil** | ***Phragmites australis*** | (Gratton & Denno, 2005) |
| | | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | **Closed** | **Soil** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| **Predators** | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | Neutral | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | Closed | Both | *Fallopia sachalinensis* | (Skubala & Mierny, 2009) |
| | | **Closed** | **Soil** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | Positive | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Closed** | **Litter** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| *Acari* (Oribatida) | Positive | **Closed** | **Soil** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | | **Closed** | **Litter** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| | | **Closed** | **Litter** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| **Detrivores** | Neutral | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | Negative | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | Closed | Both | *Fallopia sachalinensis* | (Skubala & Mierny, 2009) |
| | | **Closed** | **Soil** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| *Acari* (Actinedida) | Neutral | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| **No trophic group assigned** | Positive | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | **Closed** | **Soil** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| | | **Closed** | **Litter** | ***Quercus rubra*** | (Kohyt & Skubała, 2013) |
| *Aranea* | Positive | **Open** | **Litter** | **Multiple (litter)** | (Wolkovich *et al.*, 2009) |
| | | **Open** | **Litter** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | Closed | Litter | *Salix rubens* | (Greenwood *et al.*, 2004) |
| **Predators** | | **Closed** | **Litter** | ***Phoenix canariensis*** | (Talley *et al.*, 2012) |
| | Neutral | Open | Litter | *Chrysanthemoides monilifera* | (Wilkie *et al.*, 2007) |
| | | **Closed** | **Litter** | ***Lonicera maackiii*** | (Christopher & Cameron, 2008) |
| | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| | | **Closed** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | Negative | Both | Litter | *Campylopus introflexus* | (Schirmel *et al.*, 2011) |
| | | **Open** | **Litter** | ***Microstegium vimineum*** | (Tang *et al.*, 2012) |
| | | **Open** | **Soil** | ***Senecio jacobea*** | (Wardle *et al.*, 1995) |
| | | **Open** | **Litter** | ***Chrysanthemoiudes monilifera*** | (Lindsay & French, 2006) |
| | | **Open** | **Litter** | ***Phragmites australis*** | (Gratton & Denno, 2005) |
| | | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | Closed | Soil | *Phoenix canariensis* | (Iannone *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |
| | | Closed | Litter | *Chromolaena odorata* | (Mgobozi *et al.*, 2008) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| *Chilopoda* | Positive | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| **Predators** | Neutral | **Both** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | | **Open** | **Litter** | ***Chrysanthemoiudes monilifera*** | (Lindsay & French, 2006) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Asparagus scandens*** | (Bassett, 2014) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| | | | | ***Hedychium gardnerianum*** | |
| | | | | ***Tradescantia fluminensis*** | |
| | | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| | Negative | **Open** | **Litter** | ***Vincetoxicum rossicum*** | (Ernst & Cappuccino, 2005) |
| *Coleoptera* (total) | Positive | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | **Open** | **Litter** | ***Alternanthera philoxeroides*** | (Bassett *et al.*, 2011) |
| | | **Open** | **Litter** | ***Senecio jacobea*** | (Wardle *et al.*, 1995) |
| | | Open | Litter | *Ulex europaeus* | (Harris *et al.*, 2004) |
| **No trophic group assigned** | | Open | Litter | *Salix cinereal* | (Watts *et al.*, 2012) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| | | Closed | Litter | *Salix rubens* | (Greenwood *et al.*, 2004) |
| | | **Closed** | **Litter** | **Multiple (litter)** | (Tuttle *et al.*, 2009) |
| | Neutral | Both | Litter | Multiple | (Crisp *et al.*, 1998) |
| | | Both | Litter | Multiple | (Samways *et al.*, 1996) |
| | | **Open** | **Litter** | ***Chrysanthemoiudes monilifera*** | (Lindsay & French, 2006) |
| | | Open | Litter | *Solidago canadensis* *Solidago gigantea* | (Baranová *et al.*, 2014) |
| | | Open | Litter | *Vincetoxicum rossicum* | (Ernst & Cappuccino, 2005) |
| | | Open | Litter | *Phragmites australis* | (Gratton & Denno, 2005) |
| | | Open | Litter | *Carpobrotus acinaciformis* | (Palmer *et al.*, 2004) |
| | | Open | Litter | *Chrysanthemoides monilifera* | (Wilkie *et al.*, 2007) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Asparagus scandens*** ***Hedychium gardnerianum*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Lonicera maackiii*** | (Christopher & Cameron, 2008) |
| | | **Closed** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | | **Closed** | **Litter** | ***Microstegium vimineum*** | (McGrath & Binkley, 2009) |
| | Negative | Both | Litter | *Fallopia japonica* | (Kappes *et al.*, 2007) |
| | | **Open** | **Litter** | ***Solidago canadensis*** | (de Groot *et al.*, 2007) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| | | Open | Litter | *Prosopis glandulosa* | (Steenkamp & Chown, 1996) |
| | | Open | Litter | *Eragrostis lehmanniana* | (Litt & Steidl, 2010) |
| | | **Closed** | **Litter** | ***Phoenix canariensis*** | (Talley *et al.*, 2012) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Standish, 2004) |
| | | **Closed** | **Litter** | ***Phoenix canariensis*** | (Talley *et al.*, 2012) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| *Coleoptera* (Carabidae) | Positive | Open | Litter | *Ageratina adenophora* | (Gu *et al.*, 2008) |
| **Predators** | Neutral | **Open** | **Litter** | ***Alternanthera philoxeroides*** | (Bassett *et al.*, 2011) |
| | | Open | Litter | *Campylopus introflexus* | (Schirmel *et al.*, 2011) |
| | | **Closed** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | Negative | Open | Litter | *Solidago canadensis*<br>*Solidago gigantea* | (Baranová *et al.*, 2014) |
| | | **Open** | **Litter** | ***Solidago canadensis*** | (de Groot *et al.*, 2007) |
| | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| *Collembola* | Positive | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Open** | **Litter** | ***Senecio jacobea*** | (Wardle *et al.*, 1995) |
| | | **Closed** | **Both** | ***Microstegium vimineum*** | (Tuttle *et al.*, 2009) |
| **Microbivores** | | **Closed** | **Soil** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | Closed | Soil | *Arundo donax* | (Maceda-Veiga *et al.*, 2016) |
| | | **Closed** | **Litter** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | Neutral | **Open** | **Litter** | **Multiple (litter)** | (Wolkovich *et al.*, 2009) |
| | | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| | | Open | Soil | *Buddeja davidii* | (Peltzer *et al.*, 2009) |
| | | **Open** | **Litter** | ***Chrysanthemoides monilifera*** | (Lindsay & French, 2006) |
| | | Closed | Both | *Fallopia sachalinensis* | (Skubala & Mierny, 2009) |
| | | **Closed** | **Soil** | ***Impatiens glandulifera*** | (Rusterholz *et al.*, 2014) |
| | | **Closed** | **Litter** | ***Microstegium vimineum*** | (McGrath & Binkley, 2009) |
| | | **Closed** | **Litter** | ***Phoenix canariensis*** | (Talley *et al.*, 2012) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Standish, 2004) |
| | | **Closed** | **Litter** | ***Asparagus scandens*** ***Hedychium gardnerianum*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Lonicera maackiii*** | (Christopher & Cameron, 2008) |
| | Negative | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | **Open** | **Litter** | ***Phragmites australis*** | (Gratton & Denno, 2005) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| *Diplopoda* | Positive | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| **Detrivores** | Neutral | **Open** | **Litter** | ***Vincetoxicum rossicum*** | (Ernst & Cappuccino, 2005) |
| | | **Closed** | **Both** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | **Closed** | **Litter** | ***Asparagus scandens*** ***Hedychium gardnerianum*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| | Negative | Both | Litter | *Fallopia japonica* | (Kappes *et al.*, 2007) |
| | | Closed | Soil | *Arundo donax* | (Maceda-Veiga *et al.*, 2016) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |
| *Enchytraeids* | Positive | **Open** | **Soil** | ***Carmichaelia odorata*** | (St.John *et al.*, 2012) |
| **Detrivores** | Neutral | **Closed** | **Soil** | ***Hedychium gardnerianum*** | (Yeates & Williams, 2001) |
| | | **Closed** | **Soil** | ***Tradescantia fluminensis*** | (Yeates & Williams, 2001) |
| | Negative | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | **Closed** | **Soil** | ***Ulex europaeus*** | (Yeates & Williams, 2001) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| *Isopoda* | Positive | **Closed** | **Both** | **Litter of various invasives** | (Tuttle *et al.*, 2009) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |
| | | **Closed** | **Litter** | ***Asparagus scandens*** | (Bassett, 2014) |
| **Detrivores** | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| | | **Closed** | **Litter** | ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | Neutral | Both | Litter | *Fallopia japonica* | (Kappes *et al.*, 2007) |
| | | **Open** | **Litter** | ***Chrysanthemoides monilifera*** | (Lindsay & French, 2006) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Hedychium gardnerianum*** | (Bassett, 2014) |
| | Negative | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Closed** | **Soil** | ***Ailanthus altissima*** | (Gutiérrez-López *et al.*, 2014) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| *Oligochaeta* | Positive | **Open** | **Soil** | ***Agrostis stolonifera*** | (Gremmen *et al.*, 1998) |
| | | **Open** | **Litter** | ***Microstegium vimineum*** | (Tang *et al.*, 2012) |
| | | Open | Soil | Multiple | (Xu *et al.*, 2013) |
| **Detrivores** | | **Closed** | **Soil** | ***Berberis thunbergii*** ***Microstegium vimineum*** | (Kourtev *et al.*, 1999) |
| | Neutral | Closed | Soil | *Rhamnus cathartica* | (Iannone *et al.*, 2015) |
| | | **Closed** | **Litter** | ***Ailanthus altissima*** | (Motard *et al.*, 2015) |
| | | Closed | Litter | *Impatiens glandulifera* ***Asparagus scandens*** | (Tanner *et al.*, 2013) |
| | | **Closed** | **Litter** | ***Hedychium gardnerianum*** ***Tradescantia fluminensis*** | (Bassett, 2014) |
| | | **Closed** | **Litter** | ***Follopia* ssp.** | (Gerber *et al.*, 2008) |
| | Negative | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | Open | Soil | *Chromolaena odorata* | (Koné *et al.*, 2012) |
| | | Closed | Soil | *Ligustrum sinense* | (Lobe *et al.*, 2014) |
| | | Closed | Soil | *Rhamnus cathartica* | (Wyckoff *et al.*, 2014) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| *Opiliones* | Positive | **Open** | **Soil** | ***Senecio jacobea*** | (Wardle *et al.*, 1995) |
| **Predators** | Neutral | Both | Litter | *Fallopia japonica* | (Kappes *et al.*, 2007) |
| | | **Open** | **Litter** | ***Microstegium vimineum*** | (Tang *et al.*, 2012) |
| | Negative | **Open** | **Litter** | ***Microstegium vimineum*** | (Tang *et al.*, 2012) |
| *Hymenoptera* (Formicidae) | Positive | Open | Litter | *Carduus thoermeri*<br>*Onopordum acanthium* | (Lescano & Farji-Brener, 2011) |
| | | **Closed** | **Both** | ***Microstegium vimineum*** | (Tuttle *et al.*, 2009) |
| | | Closed | Litter | *Salix rubens* | (Greenwood *et al.*, 2004) |
| **Generalist predators** | Neutral | **Open** | **Litter** | ***Chrysanthemoides monilifera*** | (Lindsay & French, 2006) |
| | | **Open** | **Litter** | ***Phragmites australis*** | (Gratton & Denno, 2005) |
| | | **Open** | **Litter** | ***Chrysanthemoides monilifera*** | (Lindsay & French, 2006) |
| | | Open | Litter | *Andropogon gayanus* | (Parr *et al.*, 2010) |
| | | Open | Litter | *Chrysanthemoides monilifera* | (Wilkie *et al.*, 2007) |
| | | **Closed** | **Litter** | ***Phoenix canariensis*** | (Talley *et al.*, 2012) |
| | | **Closed** | **Litter** | ***Lonicera maackiii*** | (Christopher & Cameron, 2008) |
| | Negative | **Closed** | **Both** | ***Microstegium vimineum*** | (Tuttle *et al.*, 2009) |
| | | **Open** | **Litter** | **Multiple (litter)** | (Wolkovich *et al.*, 2009) |
| | | Open | Litter | *Acacia salignia* | (French & Major, 2001) |
| | | **Open** | **Litter** | ***Vincetoxicum rossicum*** | (Ernst & Cappuccino, 2005) |
| | | Closed | Litter | *Pseudotsuga menziesii* | (Finch & Szumelda, 2007) |
| | | **Closed** | **Litter** | ***Fallopia* ssp.** | (Gerber *et al.*, 2008) |
| | | Closed | Litter | *Arundo donax* | (Herrera & Dudley, 2003) |
| | | Closed | Litter | *Impatiens glandulifera* | (Tanner *et al.*, 2013) |
| *Nematoda* (Total) | Positive | **Open** | **Soil** | ***Phragmites australis*** | (Angradi *et al.*, 2001) |
| | | **Open** | **Litter** | ***Spartina alterniflora*** | (Chen *et al.*, 2007) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| | | **Open** | **NA** | **Multiple** | (Morriën *et al.*, 2012) |
| | | **Closed** | **Both** | ***Hedychium gardnerianum*** | (Yeates & Williams, 2001) |
| **No trophic group assigned** | Neutral | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap & Phillips, 2001) |
| | | **Open** | **Soil** | ***Ambrosia trifida*** | (Liang *et al.*, 2007) |
| | | **Open** | **Open** | ***Raphanus sativus*** | (Pearse *et al.*, 2014) |
| | | Open | Soil | *Buddleja davidii* | (Peltzer *et al.*, 2009) |
| | | Open | Soil | *Solidago gigantean* | (Quist *et al.*, 2014) |
| | | Open | Litter | *Solidago canadensis* | (Schittko & Wurst, 2014) |
| | | **Closed** | **Both** | ***Tradescantia fluminensis*** | (Yeates & Williams, 2001) |
| | Negative | Both | Soil | *Heracleum sosnowskyi* | (Renčo & Baležentienė, 2015) |
| | | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| | | **Open** | **Soil** | ***Melaleuca quinquenervia*** | (Porazinska *et al.*, 2007) |
| | | **Open** | **NA** | **Ageratina adenophora**<br>**Chromolaena odorata** | (Xiao *et al.*, 2013) |
| | | **Closed** | **Both** | ***Ulex europaeus*** | (Yeates & Williams, 2001) |
| *Nematoda* (Bacterivorous) | Positive | **Open** | **Soil** | ***Ambrosia trifida*** | (Liang *et al.*, 2007) |
| | | **Open** | **Litter** | ***Spartina alterniflora*** | (Chen *et al.*, 2007) |
| **Microbivores** | Neutral | **Open** | **NA** | **Multiple** | (Morriën *et al.*, 2012) |
| | | **Open** | **Open** | ***Raphanus sativus*** | (Pearse *et al.*, 2014) |
| | | **Open** | **NA** | **Ageratina adenophora**<br>**Chromolaena odorata** | (Xiao *et al.*, 2013) |
| | | **Closed** | **Both** | ***Hedychium gardnerarium*** | (Yeates & Williams, 2001) |
| | Negative | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| *Nematoda* (Root-feeders & Parasites) | Positive | **Open** | **Soil** | ***Ambrosia trifida***<br>***Hedychium gardnerianum*** | (Liang *et al.*, 2007) |
| | | **Closed** | **Both** | ***Tradescantia fluminensis***<br>***Ulex europaeus*** | (Yeates & Williams, 2001) |

| Taxa | Effect of IAS | Habitat | Soil layer | Invasive species | Reference |
|---|---|---|---|---|---|
| **Herbivores** | | | | | |
| | Neutral | **Open** | **NA** | **Multiple** | (Morriën *et al.*, 2012) |
| | | **Open** | **Litter** | ***Spartina alterniflora*** | (Chen *et al.*, 2007) |
| | | **Closed** | **Both** | ***Hedychium gardnerianum*** ***Tradescantia fluminensis*** ***Ulex europaeus*** | (Yeates & Williams, 2001) |
| | Negative | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| | | **Open** | **Soil** | ***Melaleuca quinquenervia*** | (Porazinska *et al.*, 2007) |
| | | **Open** | **NA** | **Ageratina adenophora** **Chromolaena odorata** | (Xiao *et al.*, 2013) |
| *Nematoda* (Fungivorous) | Positive | **Open** | **Soil** | ***Ambrosius trifida*** | (Liang *et al.*, 2007) |
| | | **Open** | **NA** | **Multiple** | (Morriën *et al.*, 2012) |
| **Microbivores** | Negative | **Open** | **Soil** | ***Bromus tectorum*** | (Belnap *et al.*, 2005) |
| | | **Open** | **Open** | ***Raphanus sativus*** | (Pearse *et al.*, 2014) |
| | | **Open** | **Soil** | ***Melaleuca quinquenervia*** | (Porazinska *et al.*, 2007) |
| | | **Closed** | **Both** | ***Hedychium gardnerianum*** ***Tradescantia fluminensis*** ***Ulex europaeus*** | (Yeates & Williams, 2001) |
| *Nematoda* (Predators) | Positive | **Open** | **Open** | ***Raphanus sativus*** | (Pearse *et al.*, 2014) |
| | | Open | Soil | *Buddleja davidii* | (Peltzer *et al.*, 2009) |
| **Predators** | Neutral | **Open** | **Soil** | ***Ambrosia trifida*** | (Liang *et al.*, 2007) |
| | | **Open** | **NA** | **Multiple** | (Morriën *et al.*, 2012) |
| | | **Open** | **NA** | **Ageratina adenophora** **Chromolaena odorata** | (Xiao *et al.*, 2013) |
| | | **Open** | **Litter** | ***Spartina alterniflora*** | (Chen *et al.*, 2007) |
| | | **Closed** | **Both** | ***Hedychium gardnerianum*** ***Tradescantia fluminensis*** ***Ulex europaeus*** | (Yeates & Williams, 2001) |

# Appendice C

Tab. 1: Floral data using Braun-Blanquet coding (i: not many, 1-5 individuals; +: sparsely or very sparsely present with very small cover; 1: plentiful but small cover (<5%); 2: any number of individuals covering 5-25% of the area; 3: any number of individuals covering 25-50% of the area; 4: any number of individuals covering 50-75% of the area; 5: any number of individuals covering ore than 75% of the area)

| Control | | *Castanea sativa* | | | | | | | | | | | | | | | | | | | | *Quercus petraea* | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | | Authouillet | | | | Préaux | | | | Vaunoise | | | | | | Autheuil | | | | Mélarbière | | | | Pouvrai | | | | | | | | | | |
| Modality | | Control | Mixed | Robinia | | Control | Mixed | Robinia | | Control | Mixed | Robinia | | | | Control | Mixed | Robinia | | Control | Mixed | Robinia | | Control | Mixed | Robinia | | | | | | | | |
| Codes | | ATO-CT-1 | ATO-CT-2 | ATO-CT-3 | ATO-MX-1 | ATO-MX-2 | ATO-MX-3 | ATO-RB-1 | ATO-RB-2 | ATO-RB-3 | PRX-CT-1 | PRX-CT-2 | PRX-CT-3 | PRX-MX-1 | PRX-MX-2 | PRX-MX-3 | PRX-RB-1 | PRX-RB-2 | PRX-RB-3 | VNO-CT-1 | VNO-CT-2 | VNO-CT-3 | VNO-MX-1 | VNO-MX-2 | VNO-MX-3 | VNO-RB-1 | VNO-RB-2 | VNO-RB-3 | AHE-CT-1 | AHE-CT-2 | AHE-CT-3 | AHE-MX-1 | AHE-MX-2 | AHE-MX-3 | AHE-RB-1 | AHE-RB-2 | AHE-RB-3 | MLB-CT-1 | MLB-CT-2 | MLB-CT-3 | MLB-MX-1 | MLB-MX-2 | MLB-MX-3 | MLB-RB-1 | MLB-RB-2 | MLB-RB-3 | PVR-CT-1 | PVR-CT-2 | PVR-CT-3 | PVR-MX-1 | PVR-MX-2 | PVR-MX-3 | PVR-RB-1 | PVR-RB-2 | PVR-RB-3 |
| **Species** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acer pseudoplatanus* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + | 0 | 0 | 0 | + | + | 1 | 0 | 0 | 0 | 0 | i | i | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i |
| *Adoxa moschatellina* | | + | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + | 0 | 0 | 0 | + | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Carex sylvatica* | | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Carpinus betulus* | | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Castanea sativa* | | + | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | + | 0 | + | 0 | 0 | i | + | 0 | 0 | + | 0 | 0 | i | 0 | + | 2 | 3 | 2 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chamaecystus supinus* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Circaea lutetiana* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + |
| *Corylus avenulla* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | + | 0 | 0 | i | 0 | 0 | i | 0 | 0 | 0 | i | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 1 |
| *Crataegus monogyna* | | + | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 4 | + |
| *Dryopteris carthusiana* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dryopteris dilatata* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dryopteris filix-mas* | | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Euphorbia sylvatica* | | i | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Fagus sylvatica* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Fraxinus excelsior* | | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | + | 1 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Galeopsis tetrahit* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Galium aparine* | | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Galium sylvatica* | | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | + | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | + | 0 | 0 |
| *Geranium robertianum* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | + | + | 0 | i | + | + | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hedera helix* | | 5 | 1 | 2 | + | 1 | 3 | 1 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 5 | 1 | 1 | 1 | 0 | 0 | + | 1 | 2 | 2 | 3 | 4 | 4 | 1 | + | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hyacinthoides non-scripta* | | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 1 | 2 | 3 | 1 | 2 | 0 | 4 | 4 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | + | 3 | 2 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ilex aquifolium* | | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 0 | 2 | 2 | 1 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + |
| *Impatiens noli-tangere* | | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Juncus bufonius* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lamium galeobdolon* | | 0 | 0 | 0 | 0 | 3 | 0 | + | 1 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | 0 | 0 | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ligustrum vulgare* | | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 4 | 1 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lonicera periclymenum* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Maianthemum bifolium* | | i | + | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Melica uniflora* | | 0 | 0 | 2 | 4 | 0 | 0 | 0 | 3 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | + | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Milium effusum* | | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paris quadrifolia* | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polygonum multiflorum* | | 0 | 0 | 0 | + | 0 | 0 | + | + | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 2 | 0 | + | + | 0 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pteridium aquilinum* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | + | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Quercus petraea* | | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rosa pimpinellifolia* | | + | 1 | 0 | 2 | + | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rubus fruticosus* | | 1 | 3 | 2 | 2 | + | 2 | 0 | 0 | 0 | 5 | 5 | 5 | 4 | 5 | 5 | 5 | 5 | 4 | 5 | 5 | 5 | 4 | 2 | 0 | 5 | 5 | 4 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | + | 2 | 5 | 4 | 4 | 1 | 3 | 0 | 4 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ruscus aculeatus* | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sambucus nigra* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Scrophularia nodosa* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Solidago virgaurea* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stachys sylvatica* | | 0 | 3 | 3 | 2 | 1 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | i | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 4 | 3 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stellaria holostea* | | 0 | 0 | 0 | 2 | i | 0 | 4 | 4 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Glechoma hederacea* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | i | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Urtica dioica* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | + | 0 | 0 | 0 | 0 | 0 | 1 | i | 0 | 2 | 0 | 0 | 0 | 0 | + | 0 | 0 | 0 | 1 | i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Veronica montana* | | 1 | 2 | 0 | 2 | 0 | 0 | 4 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | i | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Vinca minor* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Viola riviniana* | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Tab. 2: Faunal data on soil collembola showing abundance by species and sampling area. Values presented average values for the two samples per horizon (superficial organic (O) and organo-mineral (A)) which where then summed for analysis: V = [(O1+O2)/2] + [(A1+A2)/2]*

| Control | *Castanea sativa* | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Authouillet | | | | | | | | | Préaux | | | | | | | | | Vaunoise | | | | | | | | |
| Modality | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | |
| Codes | ATO-CT-1 | ATO-CT-2 | ATO-CT-3 | ATO-MX-1 | ATO-MX-2 | ATO-MX-3 | ATO-RB-1 | ATO-RB-2 | ATO-RB-3 | PRX-CT-1 | PRX-CT-2 | PRX-CT-3 | PRX-MX-1 | PRX-MX-2 | PRX-MX-3 | PRX-RB-1 | PRX-RB-2 | PRX-RB-3 | VNO-CT-1 | VNO-CT-2 | VNO-CT-3 | VNO-MX-1 | VNO-MX-2 | VNO-MX-3 | VNO-RB-1 | VNO-RB-2 | VNO-RB-3 |
| **Species** | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Anurida granaria* | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 1.0 | 0.5 | 0.5 | 0.0 | 0.5 |
| *Ballistura schoetti* | 0.5 | 0.5 | 1.0 | 0.5 | 0.0 | 0.5 | 1.0 | 0.0 | 1.0 | 0.5 | 0.5 | 1.0 | 0.5 | 0.5 | 0.0 | 0.0 | 1.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Cyphoderus albinus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Cryptopygus bipunctatus* | 0.5 | 1.5 | 2.0 | 2.5 | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 | 2.0 | 1.5 | 1.5 | 1.0 | 2.5 | 1.0 | 1.0 | 0.5 | 1.0 | 2.0 | 1.0 | 1.0 | 3.0 | 0.0 | 1.5 | 0.0 | 1.0 |
| *Cryptopygus garetti* | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.5 | 0.0 | 1.5 | 0.0 | 0.0 |
| *Cryptopygus scapeliferus* | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 1.5 | 0.0 |
| *Deuteraphorura scotaria* | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Entomobrya lanuginosa* | 3.5 | 2.0 | 4.0 | 9.0 | 0.5 | 6.0 | 0.0 | 0.0 | 3.5 | 6.0 | 3.5 | 8.0 | 5.0 | 2.5 | 6.0 | 1.0 | 2.0 | 2.5 | 4.0 | 4.0 | 4.5 | 5.0 | 7.0 | 2.5 | 10.5 | 1.0 | 5.0 |
| *Entomobryoides myrmecophilus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia brevicauda* | 2.5 | 1.5 | 1.5 | 8.5 | 0.0 | 2.0 | 0.0 | 0.0 | 5.0 | 3.0 | 4.0 | 5.0 | 8.5 | 2.0 | 1.0 | 1.5 | 5.0 | 0.5 | 5.0 | 2.0 | 2.0 | 1.5 | 3.0 | 2.0 | 0.5 | 0.5 | 3.0 |
| *Folsomia candida* | 0.0 | 0.5 | 0.0 | 5.5 | 0.0 | 2.0 | 1.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 |
| *Frisea claviseta* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia fimetaria* | 0.0 | 0.5 | 0.0 | 2.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.5 | 2.0 | 9.0 | 1.5 | 5.5 | 1.0 | 5.5 | 5.5 | 4.0 | 0.0 | 6.0 | 0.0 | 1.0 | 2.0 | 1.5 | 0.0 | 6.0 | 0.0 | 5.5 |
| *Folsomia inoculata* | 6.5 | 0.0 | 9.0 | 4.0 | 0.0 | 3.0 | 0.0 | 0.0 | 5.0 | 0.0 | 2.0 | 0.0 | 2.0 | 0.0 | 0.0 | 2.5 | 4.5 | 6.0 | 0.0 | 6.5 | 3.0 | 2.5 | 7.0 | 8.0 | 0.0 | 0.0 | 6.5 |
| *Folsomia litsteri* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.5 | 6.0 | 0.0 | 0.0 |
| *Folsomia manolachei* | 10.5 | 4.5 | 10.5 | 13.0 | 1.0 | 8.5 | 0.0 | 0.5 | 9.0 | 7.5 | 8.5 | 17.5 | 16.5 | 5.0 | 8.0 | 3.5 | 14.0 | 5.0 | 14.0 | 8.5 | 7.0 | 3.5 | 10.5 | 6.5 | 13.0 | 6.5 | 9.5 |
| *Frisea mirabilis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomides parvulus* | 1.0 | 0.5 | 0.5 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.5 | 1.5 | 1.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia quadrioculata* | 3.5 | 2.5 | 1.0 | 3.5 | 6.5 | 1.5 | 2.0 | 0.0 | 0.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 3.5 | 0.0 |
| *Folsomia sexoculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Folsomia spinosa* | 4.0 | 3.0 | 5.5 | 10.5 | 1.0 | 5.5 | 0.0 | 0.0 | 5.5 | 6.0 | 2.5 | 9.5 | 7.5 | 5.5 | 7.0 | 0.5 | 4.5 | 9.5 | 0.0 | 9.5 | 6.5 | 3.0 | 9.5 | 2.5 | 3.0 | 0.5 | 5.5 |
| *Frisea truncata* | 2.5 | 0.5 | 5.0 | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 1.0 | 1.0 | 1.0 | 0.5 | 0.5 | 0.0 | 2.5 | 0.5 | 0.5 | 1.0 | 0.5 | 1.0 | 0.5 | 4.0 | 0.0 | 3.5 |
| *Heteromurus nitidus* | 0.5 | 0.5 | 1.0 | 3.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 1.5 | 0.5 | 1.5 | 1.0 | 0.5 | 2.0 | 0.5 | 1.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.5 | 1.0 | 0.5 | 1.0 | 0.0 | 1.0 |
| *Isotomiella minor* | 0.5 | 0.0 | 6.0 | 0.5 | 4.5 | 0.5 | 1.0 | 1.0 | 11.0 | 2.5 | 0.5 | 5.5 | 0.0 | 10.5 | 0.5 | 2.0 | 2.5 | 3.0 | 0.0 | 10.5 | 8.0 | 10.5 | 9.5 | 8.5 | 2.0 | 4.5 | 7.5 |
| *Isotomurus palustris* | 1.5 | 0.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 2.0 | 1.0 | 0.5 | 1.0 | 0.5 | 1.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 1.0 | 1.0 | 0.0 | 1.0 |
| *Isotomodes productus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Isotoma viridis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Lepidocyrtus cyaneus* | 1.0 | 1.0 | 1.0 | 2.0 | 0.5 | 1.5 | 0.5 | 0.5 | 1.5 | 1.0 | 0.5 | 1.5 | 1.5 | 1.5 | 1.5 | 0.0 | 1.5 | 0.5 | 1.5 | 1.0 | 2.0 | 0.5 | 0.0 | 1.0 | 1.0 | 0.0 | 1.0 |
| *Lepidocyrtus lanuginosus* | 0.0 | 2.0 | 2.5 | 2.0 | 0.0 | 1.0 | 0.0 | 0.5 | 0.5 | 0.5 | 2.0 | 1.5 | 1.0 | 0.5 | 4.5 | 0.0 | 0.5 | 2.0 | 0.0 | 0.5 | 0.5 | 1.0 | 1.0 | 2.0 | 0.5 | 0.5 | 0.5 |
| *Lathriopyga longiseta* | 3.5 | 0.0 | 0.5 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 3.5 | 0.0 | 0.5 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 4.0 | 3.5 | 0.0 | 0.5 | 0.0 |
| *Lepidocyrtus ruber* | 0.5 | 0.5 | 1.0 | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 1.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 1.0 | 0.5 | 0.5 | 0.5 | 0.0 |
| *Metaphorura affinis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Monobella grassei* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Mesaphorura macrochaeta* | 8.5 | 9.5 | 11.5 | 16.5 | 0.0 | 13.5 | 0.0 | 2.5 | 13.5 | 12.0 | 21.5 | 13.0 | 17.0 | 5.5 | 12.5 | 5.0 | 11.5 | 5.5 | 4.5 | 12.5 | 6.5 | 9.0 | 15.5 | 11.0 | 3.0 | 3.5 | 16.0 |
| *Megalothorax minimus* | 6.0 | 1.0 | 3.5 | 11.5 | 0.0 | 6.0 | 1.0 | 0.0 | 5.0 | 8.0 | 5.0 | 8.0 | 8.0 | 2.5 | 10.0 | 0.0 | 8.0 | 3.0 | 0.5 | 5.0 | 0.0 | 0.5 | 0.0 | 3.0 | 7.5 | 1.5 | 11.0 |
| *Micranurida pygmaea* | 3.0 | 0.5 | 2.0 | 3.5 | 0.0 | 1.0 | 0.0 | 1.0 | 2.0 | 1.5 | 3.0 | 3.5 | 1.5 | 1.0 | 4.0 | 0.5 | 1.5 | 0.5 | 3.0 | 1.5 | 0.0 | 0.0 | 0.0 | 1.0 | 4.5 | 1.0 | 3.0 |
| *Neelus murinus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Neanura muscorum* | 0.5 | 1.0 | 1.0 | 0.5 | 0.0 | 36.0 | 0.0 | 0.0 | 14.5 | 0.0 | 0.0 | 0.0 | 20.5 | 20.5 | 21.5 | 0.0 | 1.0 | 0.0 | 35.5 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.5 |
| *Onychiuroides granulosus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| *Pseudosinella alba* | 0.0 | 2.0 | 0.0 | 0.5 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Protaphorura armata* | 6.0 | 0.0 | 7.0 | 3.0 | 0.5 | 0.0 | 0.0 | 2.5 | 1.5 | 3.5 | 3.0 | 3.0 | 4.0 | 6.0 | 6.0 | 2.5 | 0.0 | 4.5 | 5.0 | 4.0 | 0.0 | 3.0 | 6.0 | 3.0 | 2.5 | 3.5 | 3.0 |
| *Protaphorura auriantiaca* | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 |
| *Paratullbergia callipygos* | 6.5 | 0.5 | 0.0 | 11.0 | 0.0 | 2.0 | 0.5 | 0.5 | 5.0 | 5.5 | 10.0 | 4.0 | 11.0 | 7.0 | 5.0 | 3.0 | 9.5 | 6.5 | 6.5 | 3.0 | 3.5 | 7.0 | 9.0 | 3.0 | 3.0 | 0.5 | 2.5 |
| *Pseudosinella duodecimocellata* | 0.5 | 0.0 | 1.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pseudosinella fallax* | 1.5 | 0.5 | 1.0 | 1.5 | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 | 1.0 | 1.5 | 1.5 | 2.0 | 1.0 | 2.5 | 0.5 | 1.5 | 0.5 | 0.5 | 1.5 | 0.5 | 0.5 | 1.5 | 0.5 | 1.0 | 0.5 | 2.5 |
| *Pseudosinella immaculata* | 1.5 | 0.5 | 1.0 | 2.0 | 1.0 | 1.5 | 0.0 | 0.0 | 1.0 | 2.0 | 1.0 | 1.5 | 1.5 | 0.5 | 1.5 | 0.5 | 1.5 | 0.5 | 1.0 | 1.0 | 0.5 | 0.0 | 1.0 | 0.5 | 1.0 | 0.0 | 1.0 |
| *Proisotoma minuta* | 1.0 | 0.5 | 1.5 | 4.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 3.0 | 0.0 | 0.0 | 1.0 | 6.0 | 1.5 | 1.5 | 0.5 | 0.5 | 0.5 | 0.5 | 1.0 |
| *Parisotoma notabilis* | 13.5 | 4.0 | 7.5 | 23.0 | 0.0 | 0.0 | 0.0 | 1.5 | 9.0 | 22.5 | 0.0 | 13.0 | 7.5 | 18.5 | 12.0 | 13.0 | 1.5 | 0.0 | 14.0 | 18.0 | 3.5 | 6.0 | 9.5 | 27.5 | 40.0 | 7.0 | 12.0 |
| *Pseudosinella octopunctata* | 0.5 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 2.5 | 4.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 1.0 |
| *Pseudoisotoma sensibilis* | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pseudosinella sexoculata* | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 1.0 | 1.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 |
| *Sinella curviseta* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sminthurinus elegans* | 0.5 | 0.5 | 0.5 | 1.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 1.0 | 0.5 | 2.0 | 0.5 | 0.5 | 0.0 | 1.5 | 0.0 | 0.0 |
| *Supraphorura furcifera* | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Sminthurinus niger* | 0.0 | 0.0 | 1.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 1.0 | 0.0 | 1.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 |
| *Sphaeridia pumilis* | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 1.5 | 0.0 | 0.5 | 1.0 | 1.0 | 0.0 | 0.5 | 0.0 | 0.5 |
| *Sminthurides schoetti* | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 1.5 | 4.5 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 |
| *Schoettella ununguiculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Stenacidia violacea* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Juvenile tomocerus* | 2.0 | 3.0 | 3.0 | 4.0 | 0.0 | 3.0 | 0.0 | 0.0 | 3.0 | 3.0 | 3.0 | 7.0 | 3.0 | 4.0 | 8.0 | 1.0 | 6.0 | 1.0 | 4.0 | 5.0 | 3.0 | 1.0 | 4.0 | 3.0 | 3.5 | 0.5 | 2.0 |
| *Tomocerus minutus* | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 3.5 | 0.0 | 0.0 | 0.5 | 0.5 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Tomocerus minor* | 0.5 | 0.0 | 0.5 | 0.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.5 | 1.0 | 1.0 | 1.0 | 0.0 | 1.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 0.0 | 0.5 |
| *Tomocerus vulgaris* | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 1.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 1.0 | 0.0 | 1.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Willowsia buski* | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 |
| *Xenylla boerneri* | 1.0 | 3.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 6.5 | 6.5 | 5.5 | 12.0 | 4.5 | 3.0 | 8.5 | 0.0 | 5.5 | 0.0 | 6.5 | 0.0 | 3.5 | 1.5 | 3.0 | 1.0 | 4.5 | 0.0 | 0.0 |

*Tab. 2: continued*

| Control | *Quercus petraea* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Autheuil | | | | | | | | | Mélarbière | | | | | | | | | Pouvrai | | | | | | |
| Modality | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | |
| Codes | AHE-CT-1 | AHE-CT-2 | AHE-CT-3 | AHE-MX-1 | AHE-MX-2 | AHE-MX-3 | AHE-RB-1 | AHE-RB-2 | AHE-RB-3 | MLB-CT-1 | MLB-CT-2 | MLB-CT-3 | MLB-MX-1 | MLB-MX-2 | MLB-MX-3 | MLB-RB-1 | MLB-RB-2 | MLB-RB-3 | PVR-CT-1 | PVR-CT-2 | PVR-CT-3 | PVR-MX-1 | PVR-MX-2 | PVR-MX-3 | PVR-RB-1 | PVR-RB-2 | PVR-RB-3 |
| **Species** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Anurida granaria* | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 | 1.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 1.0 | 1.0 | 0.5 | 0.5 | 2.0 | 0.0 | 1.0 |
| *Ballistura schoetti* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.5 | 1.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 1.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.5 |
| *Cyphoderus albinus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Cryptopygus bipunctatus* | 1.0 | 0.5 | 1.0 | 0.5 | 2.0 | 0.5 | 1.0 | 1.5 | 1.0 | 2.0 | 1.0 | 1.0 | 1.0 | 2.0 | 1.5 | 0.0 | 1.5 | 1.5 | 2.5 | 4.0 | 4.0 | 1.5 | 1.5 | 1.5 | 1.5 | 3.0 | 2.5 |
| *Cryptopygus garetti* | 1.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.5 | 0.5 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 3.5 | 0.5 | 1.0 | 2.0 | 0.0 |
| *Cryptopygus scapeliferus* | 0.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.0 |
| *Deuteraphorura scotaria* | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Entomobrya lanuginosa* | 1.5 | 1.0 | 3.0 | 0.5 | 6.5 | 2.0 | 2.5 | 5.5 | 2.5 | 2.5 | 1.5 | 8.0 | 5.0 | 2.0 | 13.0 | 1.5 | 2.5 | 5.5 | 9.0 | 5.5 | 4.5 | 4.0 | 5.0 | 4.0 | 11.0 | 6.5 | 6.5 |
| *Entomobryoides myrmecophilus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia brevicauda* | 5.0 | 0.0 | 3.5 | 0.0 | 2.5 | 1.5 | 7.5 | 7.0 | 2.5 | 4.0 | 3.5 | 6.5 | 6.0 | 2.0 | 8.0 | 0.0 | 3.5 | 2.0 | 6.0 | 3.5 | 9.0 | 2.0 | 5.0 | 2.0 | 9.0 | 3.0 | 5.5 |
| *Folsomia candida* | 0.0 | 0.0 | 9.5 | 0.5 | 0.0 | 0.0 | 2.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 1.0 | 15.0 | 0.0 | 11.0 | 0.0 | 0.0 | 4.5 | 1.0 | 5.5 | 9.5 | 0.0 |
| *Frisea claviseta* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia fimetaria* | 0.5 | 0.0 | 2.0 | 0.0 | 2.0 | 0.5 | 2.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 2.5 | 1.5 | 7.0 | 0.0 | 2.5 | 2.5 | 0.0 | 3.0 | 7.0 | 0.5 | 2.5 | 2.0 | 2.5 | 0.5 | 0.0 |
| *Folsomia inoculata* | 0.0 | 0.0 | 0.0 | 0.0 | 6.5 | 0.0 | 0.0 | 4.5 | 2.0 | 0.0 | 0.0 | 2.5 | 0.0 | 6.5 | 2.5 | 6.5 | 0.0 | 0.0 | 13.0 | 0.0 | 3.0 | 2.5 | 10.5 | 0.0 | 4.5 | 3.0 | 11.5 |
| *Folsomia litsteri* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Folsomia manolachei* | 5.0 | 0.0 | 14.0 | 1.0 | 12.0 | 5.0 | 9.0 | 19.0 | 11.0 | 16.0 | 3.5 | 12.0 | 12.5 | 9.5 | 23.5 | 0.0 | 7.0 | 8.5 | 16.5 | 16.0 | 19.0 | 11.5 | 12.0 | 8.0 | 20.0 | 19.0 | 17.0 |
| *Frisea mirabilis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 1.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.0 |
| *Folsomides parvulus* | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 1.5 | 0.5 | 1.0 | 0.5 | 1.0 | 1.0 | 1.0 | 1.0 | 0.0 | 0.5 | 1.0 | 2.0 | 1.0 | 1.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.5 | 1.0 |
| *Folsomia quadrioculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.5 | 0.0 | 1.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.5 | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 6.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Folsomia sexoculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 |
| *Folsomia spinosa* | 6.5 | 0.0 | 0.0 | 0.0 | 4.5 | 3.0 | 3.0 | 16.0 | 4.5 | 12.5 | 3.0 | 8.5 | 9.5 | 6.5 | 9.0 | 0.0 | 9.5 | 7.5 | 8.0 | 11.5 | 5.5 | 6.0 | 3.0 | 9.5 | 7.0 | 10.0 | 9.0 |
| *Frisea truncata* | 0.5 | 0.0 | 0.0 | 0.5 | 1.0 | 2.5 | 0.5 | 3.5 | 0.5 | 2.0 | 0.5 | 2.0 | 0.0 | 1.5 | 2.5 | 0.0 | 1.0 | 0.5 | 1.5 | 3.5 | 1.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.5 |
| *Heteromurus nitidus* | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 1.0 | 0.0 | 1.5 | 0.5 | 1.5 | 0.5 | 1.5 | 1.0 | 1.5 | 0.0 | 0.0 | 0.5 | 0.5 | 1.5 | 0.5 | 1.0 | 0.5 | 1.0 | 1.0 | 1.0 | 0.5 | 0.5 |
| *Isotomiella minor* | 3.5 | 0.0 | 14.5 | 4.0 | 12.5 | 9.0 | 32.5 | 11.0 | 9.5 | 3.5 | 0.5 | 8.0 | 0.0 | 0.5 | 14.5 | 3.5 | 9.5 | 8.5 | 10.0 | 5.0 | 9.0 | 0.5 | 0.0 | 0.0 | 16.5 | 5.0 | 0.0 |
| *Isotomurus palustris* | 0.5 | 0.0 | 0.0 | 0.0 | 1.0 | 0.5 | 1.5 | 2.0 | 1.0 | 1.5 | 0.5 | 1.5 | 0.5 | 0.5 | 2.5 | 0.0 | 0.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.0 | 0.0 | 0.5 | 0.5 | 0.0 | 1.5 |
| *Isotomodes productus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Isotoma viridis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Lepidocyrtus cyaneus* | 0.5 | 0.0 | 0.5 | 0.0 | 1.5 | 0.5 | 0.5 | 1.0 | 0.5 | 1.0 | 0.5 | 2.0 | 2.5 | 1.0 | 1.5 | 0.0 | 1.0 | 1.0 | 2.0 | 2.5 | 2.0 | 0.5 | 2.0 | 1.0 | 1.0 | 1.5 | 2.5 |
| *Lepidocyrtus lanuginosus* | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.5 | 0.5 | 1.5 | 0.5 | 0.5 | 0.0 | 1.0 | 0.5 | 2.5 | 1.0 | 0.0 | 0.5 | 0.5 | 2.0 | 2.5 | 3.0 | 0.5 | 0.0 | 0.5 | 2.5 | 0.5 | 3.0 |
| *Lathriopyga longiseta* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 0.0 | 4.0 | 3.5 | 3.5 |
| *Lepidocyrtus ruber* | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 1.0 | 0.5 | 1.5 | 0.0 | 0.5 | 0.0 | 1.0 | 1.0 | 1.5 | 0.5 | 0.5 | 0.5 | 1.5 | 0.5 | 0.5 |
| *Metaphorura affinis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Monobella grassei* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Mesaphorura macrochaeta* | 2.0 | 2.5 | 8.0 | 1.5 | 13.5 | 8.5 | 7.0 | 16.5 | 13.5 | 11.0 | 7.5 | 26.0 | 6.0 | 13.5 | 10.0 | 9.0 | 14.0 | 6.5 | 28.5 | 5.5 | 19.0 | 6.5 | 5.5 | 8.5 | 23.5 | 6.5 | 18.5 |
| *Megalothorax minimus* | 0.5 | 1.0 | 3.0 | 5.5 | 3.0 | 2.5 | 4.5 | 6.5 | 8.0 | 2.5 | 3.0 | 8.5 | 8.5 | 6.5 | 6.0 | 0.0 | 6.0 | 3.0 | 10.5 | 2.5 | 8.5 | 5.5 | 6.0 | 2.5 | 8.0 | 8.0 | 16.0 |
| *Micranurida pygmaea* | 0.5 | 0.0 | 0.5 | 0.0 | 2.5 | 1.5 | 0.5 | 1.5 | 0.5 | 2.5 | 1.5 | 0.5 | 2.0 | 1.5 | 2.5 | 0.0 | 2.0 | 1.0 | 2.0 | 4.0 | 3.5 | 1.0 | 1.5 | 1.5 | 2.5 | 2.5 | 3.5 |
| *Neelus murinus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Neanura muscorum* | 14.5 | 0.0 | 14.5 | 1.0 | 15.0 | 0.5 | 14.5 | 0.0 | 14.5 | 0.0 | 0.5 | 0.0 | 49.5 | 0.0 | 16.0 | 0.0 | 1.0 | 1.5 | 0.0 | 2.0 | 15.5 | 0.5 | 16.0 | 1.0 | 2.5 | 16.0 | 0.0 |
| *Onychiuroides granulosus* | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 |
| *Pseudosinella alba* | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 1.0 | 0.0 | 0.0 | 1.5 | 0.0 | 2.0 | 0.0 | 1.0 | 2.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| *Protaphorura armata* | 0.0 | 0.0 | 0.5 | 0.0 | 5.5 | 9.5 | 0.5 | 7.0 | 3.5 | 4.5 | 3.5 | 7.5 | 0.0 | 4.5 | 2.5 | 0.0 | 1.5 | 3.0 | 10.0 | 2.5 | 2.5 | 4.0 | 0.0 | 4.5 | 5.0 | 1.5 | 10.0 |
| *Protaphorura auriantiaca* | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Paratullbergia callipygos* | 7.0 | 4.5 | 1.5 | 1.0 | 3.0 | 7.5 | 12.0 | 9.5 | 4.5 | 6.0 | 3.5 | 3.0 | 5.5 | 7.0 | 12.5 | 0.0 | 7.0 | 9.0 | 7.0 | 12.0 | 14.0 | 6.5 | 12.0 | 4.0 | 6.0 | 9.0 | 8.0 |
| *Pseudosinella duodecimocellata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Pseudosinella fallax* | 0.5 | 0.0 | 0.5 | 0.0 | 1.0 | 0.5 | 1.0 | 2.0 | 1.5 | 1.5 | 0.5 | 2.5 | 1.5 | 1.5 | 2.5 | 0.0 | 0.5 | 1.0 | 2.0 | 0.5 | 2.5 | 1.0 | 0.5 | 0.5 | 3.0 | 1.0 | 1.5 |
| *Pseudosinella immaculata* | 1.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 2.5 | 1.0 | 1.0 | 0.5 | 1.5 | 1.5 | 1.5 | 2.0 | 0.0 | 1.0 | 1.0 | 2.5 | 2.0 | 2.0 | 1.0 | 2.5 | 1.0 | 1.5 | 1.5 | 1.5 |
| *Proisotoma minuta* | 1.5 | 0.0 | 1.0 | 0.0 | 1.0 | 3.5 | 3.0 | 2.0 | 3.5 | 3.0 | 0.0 | 3.5 | 1.5 | 1.5 | 1.0 | 0.0 | 2.0 | 4.0 | 5.0 | 4.0 | 0.5 | 1.5 | 0.5 | 1.0 | 1.0 | 0.5 | 1.5 |
| *Parisotoma notabilis* | 26.5 | 2.5 | 3.5 | 1.0 | 7.5 | 2.5 | 11.5 | 29.5 | 8.5 | 14.0 | 5.5 | 5.5 | 20.5 | 10.0 | 37.5 | 0.5 | 26.5 | 26.5 | 0.0 | 45.5 | 24.5 | 7.5 | 17.5 | 7.0 | 7.5 | 51.5 | 7.0 |
| *Pseudosinella octopunctata* | 0.5 | 0.0 | 4.0 | 0.0 | 4.0 | 0.5 | 0.0 | 2.5 | 2.0 | 0.0 | 0.0 | 0.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.5 | 0.0 | 1.0 | 0.0 | 0.5 | 0.0 | 0.0 | 4.0 | 2.0 | 0.0 | 1.0 |
| *Pseudoisotoma sensibilis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.0 |
| *Pseudosinella sexoculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 0.5 | 0.5 | 0.5 | 1.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 1.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 |
| *Sinella curviseta* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.5 | 1.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Sminthurinus elegans* | 1.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 0.0 | 2.0 | 0.5 | 1.0 | 1.0 | 1.0 | 1.0 | 1.0 | 0.0 |
| *Supraphorura furcifera* | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 |
| *Sminthurinus niger* | 1.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.5 | 1.0 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 1.5 | 0.5 | 0.5 |
| *Sphaeridia pumilis* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.0 | 0.0 | 2.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 1.0 | 1.0 | 0.0 | 1.5 | 0.5 | 0.0 |
| *Sminthurides schoetti* | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 1.5 | 1.5 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 1.5 | 0.0 | 1.5 | 0.0 | 1.5 | 3.0 | 0.0 | 0.0 |
| *Schoettella ununguiculata* | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 |
| *Stenacidia violacea* | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Juvenile tomocerus* | 2.0 | 0.0 | 0.0 | 5.5 | 4.0 | 2.0 | 2.0 | 7.0 | 4.0 | 4.0 | 1.0 | 7.0 | 7.0 | 3.0 | 11.0 | 0.0 | 5.0 | 3.0 | 7.0 | 5.0 | 7.0 | 3.0 | 2.0 | 2.0 | 7.0 | 7.0 | 7.0 |
| *Tomocerus minutus* | 1.0 | 0.0 | 0.0 | 3.5 | 0.0 | 1.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 7.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 3.5 | 1.5 | 1.0 | 0.0 | 0.5 | 0.0 |
| *Tomocerus minor* | 0.5 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 0.5 | 0.0 | 0.5 | 1.0 | 0.5 | 1.5 | 0.5 | 0.5 | 1.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| *Tomocerus vulgaris* | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 2.0 | 0.5 | 2.0 | 0.5 | 0.5 | 0.5 | 0.0 | 2.0 | 0.5 | 0.5 | 1.0 | 1.5 | 2.5 | 1.0 | 0.0 |
| *Willowsia buski* | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.5 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 |
| *Xenylla boerneri* | 0.0 | 0.0 | 6.5 | 11.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 1.0 | 0.0 | 1.0 | 4.5 | 1.0 | 4.0 | 5.5 | 1.0 | 0.0 | 0.0 | 17.5 | 0.0 | 4.5 | 4.0 | 4.0 | 7.5 | 12.0 | 12.0 |

*Tab. 3: Faunal data on the soil macrofauna abundance by species, order or site. Values presented are the sum of abundances in superficial organic (O) and organo-mineral (A) horizons.*

| Control | *Castanea sativa* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Authouillet | | | | | | | | | Préaux | | | | | | | | | Vaunoise | | | | | | |
| Modality | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | |
| Codes | ATO-CT-1 | ATO-CT-2 | ATO-CT-3 | ATO-MX-1 | ATO-MX-2 | ATO-MX-3 | ATO-RB-1 | ATO-RB-2 | ATO-RB-3 | PRX-CT-1 | PRX-CT-2 | PRX-CT-3 | PRX-MX-1 | PRX-MX-2 | PRX-MX-3 | PRX-RB-1 | PRX-RB-2 | PRX-RB-3 | VNO-CT-1 | VNO-CT-2 | VNO-CT-3 | VNO-MX-1 | VNO-MX-2 | VNO-MX-3 | VNO-RB-1 | VNO-RB-2 | VNO-RB-3 |
| **Species** | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Acari | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Aranae | 2 | 3 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 2 | 2 |
| Coleoptera | 4 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| Coleoptera larvae | 2 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 5 | 2 | 2 | 0 | 2 | 0 | 0 | 1 | 3 | 1 | 0 | 1 | 1 |
| Diptera | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera larvae | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Gasteropoda | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hymenoptera | 8 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 |
| Hymenoptera larvae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Juvenile Annelida | 5 | 2 | 6 | 4 | 4 | 1 | 5 | 2 | 6 | 45 | 22 | 13 | 2 | 11 | 2 | 23 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Juvenile Geophilomorpha | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Juvenile Lithobiomorpha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mecoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Opiliones | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 |
| Pseudoscorpiones | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Allolobophora chlorotica* | 0 | 3 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Allolobophoridella eiseni* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea longa* | 0 | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea caliginosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea chlorotica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea rosea* | 0 | 3 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arianta arbustorum* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arion empiricum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arion intermedius* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arion silvaticus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Armadillidium pictum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Armadillidium vulgare* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cochlodina laminata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Cryptops hortensis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 7 | 0 | 2 | 4 | 1 | 2 | 2 | 1 | 2 |
| *Cylindroiulus londinensis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 |
| *Cylindroiulus punctatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dendrobaena attemsi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 8 | 2 | 0 | 13 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dendrobaena octaedra* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Discus rotundatus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Geophilus easoni* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Geophilus flavus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Glomeris marginata* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Haplophthalmus montivagus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Helix aspersa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ligidium hypnorum* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius calcaratus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius crassipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius macilentus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius microps* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius penegrinus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius tenebrosus* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lumbricus castaneus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lumbricus friendi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lumbricus rubellus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Octolasion cyaneum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Octolasion lacteum* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Oniscus asellus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 8 | 2 | 0 | 5 | 1 | 1 | 2 | 8 | 3 | 10 | 10 | 4 | 2 | 5 | 2 |
| *Philoscia muscorum* | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 7 | 8 | 4 | 10 | 2 | 3 | 17 | 10 | 4 |
| *Polydesmus angustus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Polydesmus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Porcellio scaber* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 9 | 4 | 7 | 8 | 5 |
| *Porcellio spinicornis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Stigmatogaster subterranea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Strigamia acuminata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Strigamia crassipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Trichoniscus pusillus* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 9 | 0 | 1 | 0 | 0 | 3 | 2 | 0 | 3 | 0 | 0 |
| *Vertigo pusilla* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |

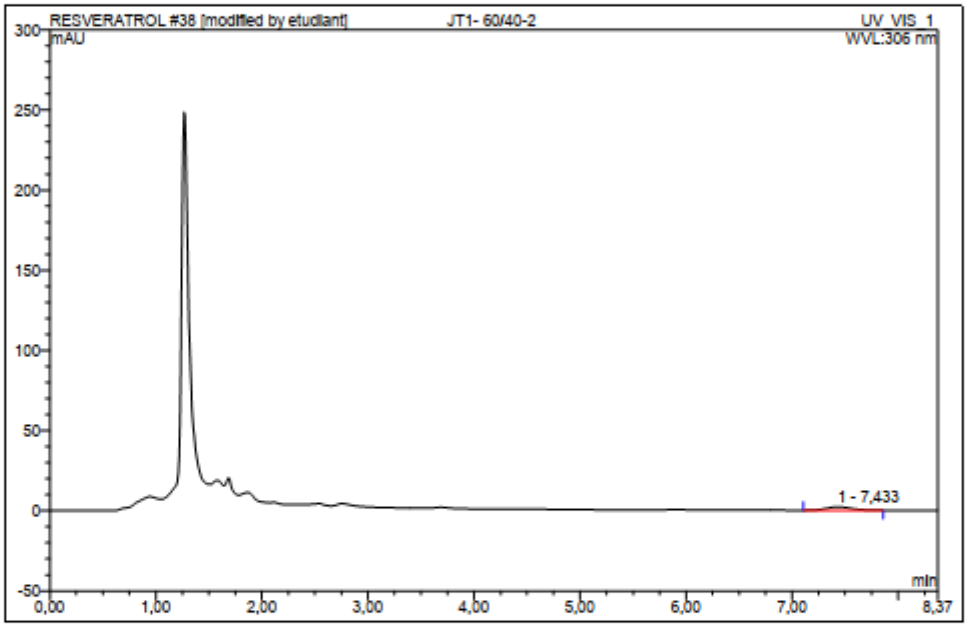
*Tab. 3: continued*

| Control | *Quercus petraea* | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Autheuil | | | | | | | | | Mélarbière | | | | | | | | | Pouvrai | | | | | | | | |
| Modality | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | | Control | | | Mixed | | | Robinia | | |
| Codes | AHE-CT-1 | AHE-CT-2 | AHE-CT-3 | AHE-MX-1 | AHE-MX-2 | AHE-MX-3 | AHE-RB-1 | AHE-RB-2 | AHE-RB-3 | MLB-CT-1 | MLB-CT-2 | MLB-CT-3 | MLB-MX-1 | MLB-MX-2 | MLB-MX-3 | MLB-RB-1 | MLB-RB-2 | MLB-RB-3 | PVR-CT-1 | PVR-CT-2 | PVR-CT-3 | PVR-MX-1 | PVR-MX-2 | PVR-MX-3 | PVR-RB-1 | PVR-RB-2 | PVR-RB-3 |
| **Species** | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Acari | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aranae | 0 | 0 | 1 | 0 | 1 | 1 | 4 | 1 | 1 | 2 | 0 | 3 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 1 |
| Coleoptera | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 5 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |
| Coleoptera larvae | 2 | 0 | 0 | 1 | 1 | 2 | 1 | 3 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 3 | 4 | 2 | 0 | 4 | 4 | 0 | 0 | 3 |
| Diptera | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| Diptera larvae | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 3 | 8 | 0 | 0 | 0 | 2 | 1 | 1 |
| Gasteropoda | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hymenoptera | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 6 | 0 | 0 | 0 | 3 | 10 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 4 | 1 |
| Hymenoptera larvae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| Juvenile Annelida | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 8 | 7 | 3 | 5 | 4 | 1 | 0 | 1 | 2 | 1 | 3 | 5 | 2 | 9 | 2 | 6 |
| Juvenile Geophilomorpha | 2 | 2 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 3 | 5 | 2 | 0 | 3 | 2 | 1 | 1 |
| Juvenile Lithobiomorpha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Mecoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Opiliones | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pseudoscorpiones | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Allolobophora chlorotica* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 6 | 0 | 1 |
| *Allolobophoridella eiseni* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea longa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 0 |
| *Aporrectodea caliginosa* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Aporrectodea chlorotica* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aporrectodea rosea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 1 |
| *Arianta arbustorum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arion empiricum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Arion intermedius* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arion silvaticus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 2 | 0 | 1 |
| *Armadillidium pictum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Armadillidium vulgare* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cochlodina laminata* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cryptops hortensis* | 0 | 0 | 0 | 3 | 6 | 2 | 4 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 6 | 2 | 2 | 3 | 4 | 5 | 3 |
| *Cylindroiulus londinensis* | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Cylindroiulus punctatus* | 2 | 1 | 2 | 0 | 2 | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Dendrobaena attemsi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dendrobaena octaedra* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Discus rotundatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Geophilus easoni* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Geophilus flavus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Glomeris marginata* | 0 | 0 | 0 | 1 | 2 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Haplophthalmus montivagus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Helix aspersa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ligidium hypnorum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius calcaratus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius crassipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lithobius macilentus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lithobius microps* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lithobius penegrinus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lithobius tenebrosus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lumbricus castaneus* | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 |
| *Lumbricus friendi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Lumbricus rubellus* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Octolasion cyaneum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Octolasion lacteum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 4 |
| *Oniscus asellus* | 4 | 1 | 3 | 6 | 14 | 0 | 11 | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 6 | 1 | 3 |
| *Philoscia muscorum* | 6 | 7 | 3 | 8 | 5 | 6 | 8 | 26 | 4 | 1 | 5 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 2 | 6 | 2 | 2 | 1 | 1 | 2 | 2 |
| *Polydesmus angustus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polydesmus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Porcellio scaber* | 9 | 3 | 2 | 52 | 9 | 2 | 22 | 42 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 |
| *Porcellio spinicornis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Stigmatogaster subterranea* | 4 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 3 | 0 | 2 | 0 |
| *Strigamia acuminata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Strigamia crassipes* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Trichoniscus pusillus* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 2 | 0 | 1 | 2 | 0 | 5 | 1 | 0 | 2 | 2 | 2 | 2 | 2 |
| *Vertigo pusilla* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

## Appendice D

**38 JT1- 60/40-2**

| | | | |
|---|---|---|---|
| *Sample Name:* | **JT1- 60/40-2** | *Injection Volume:* | **20,0** |
| *Vial Number:* | **47** | *Channel:* | **UV_VIS_1** |
| *Sample Type:* | **unknown** | *Wavelength:* | **306** |
| *Control Program:* | **resveratrol** | *Bandwidth:* | **n.a.** |
| *Quantif. Method:* | **TP Licence** | *Dilution Factor:* | **1,0000** |
| *Recording Time:* | **4/12/2015 12:56** | *Sample Weight:* | **1,0000** |
| *Run Time (min):* | **8,37** | *Sample Amount:* | **1,0000** |




| No. | Ret.Time min | Height mAU | Area mAU*min | Asymmetry(EP) | Peak Width min |
|---|---|---|---|---|---|
| 1 | 7,43 | 2,096 | 0,568 | 1,18 | 0,43 |

*Figure 1 : Chromatogram of unfiltered Knotweed Rhizome Extract (KRE). Results are from high-performance liquid chromatography with a UV detector set at 306 nm and a 60/40 water:acetonytril mobile phase through a C18 column. We used commercially available resveratrol for calibration.*

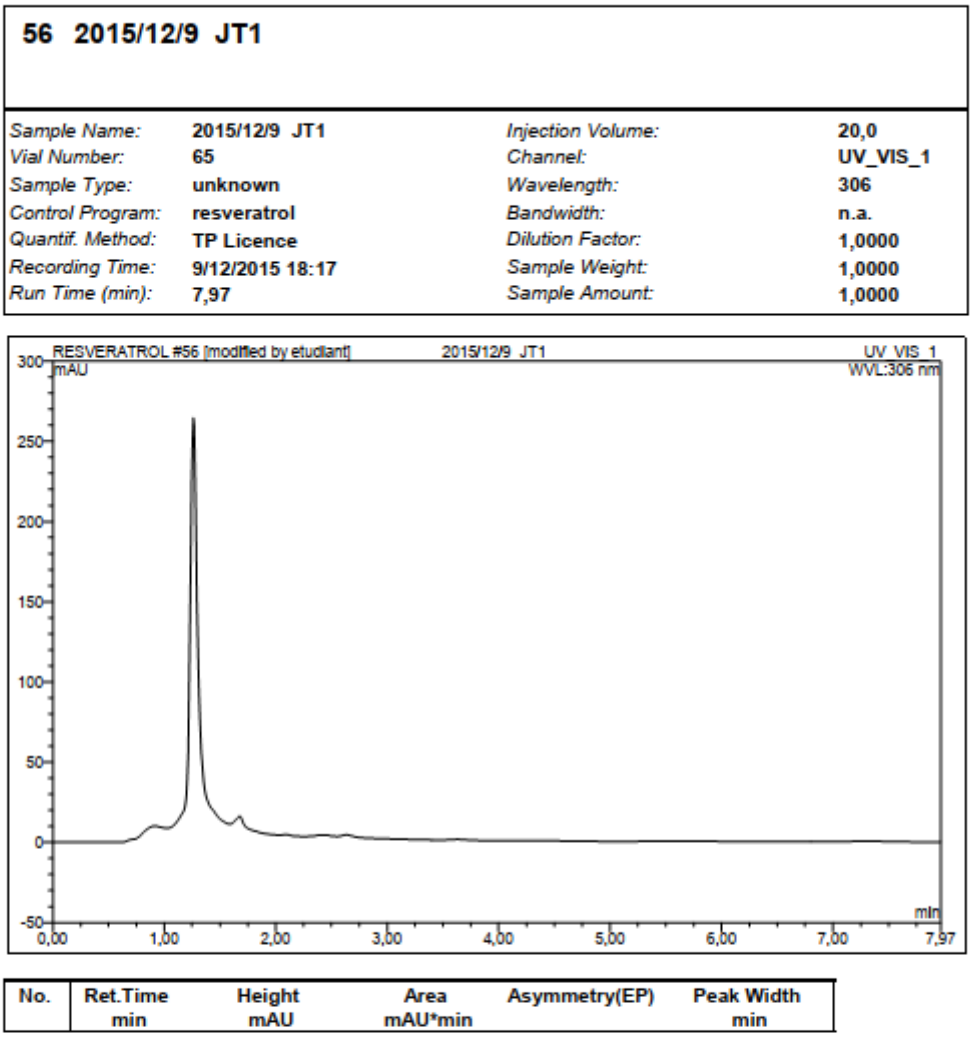
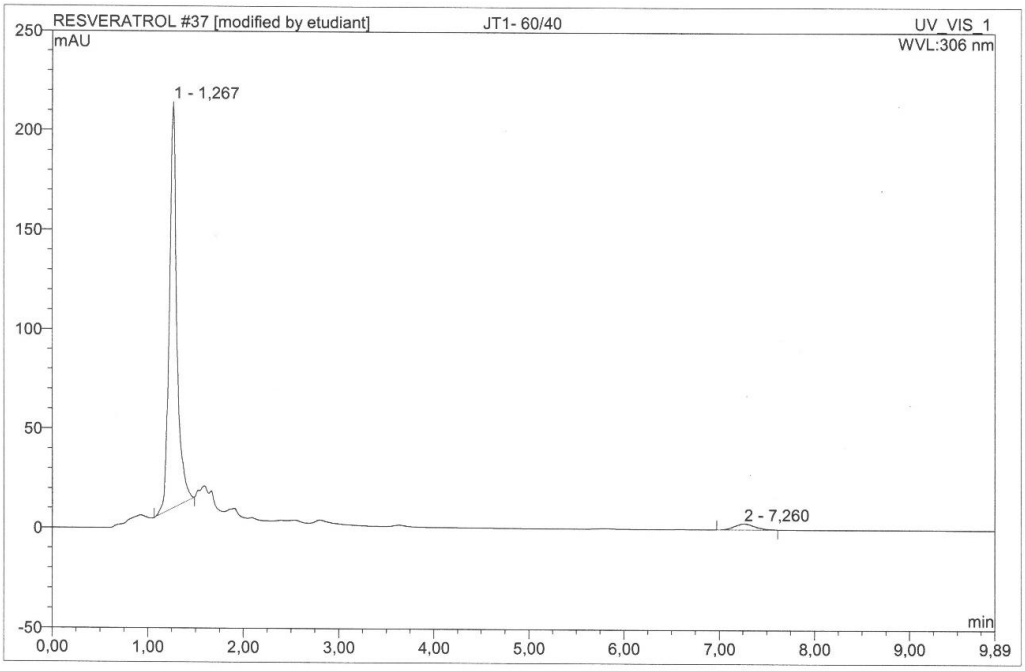



*Figure 2: Chromatogram of filtered Knotweed Rhizome Extract (KRE). Results are from high-performance liquid chromatography with a UV detector set at 306 nm and a 60/40 water:acetonytril mobile phase through a C18 column. We used commercially available resveratrol for calibration.*

**37 JT1- 60/40**

| | | | |
|---|---|---|---|
| *Sample Name:* | **JT1- 60/40** | *Injection Volume:* | **20,0** |
| *Vial Number:* | **46** | *Channel:* | **UV_VIS_1** |
| *Sample Type:* | **unknown** | *Wavelength:* | **306** |
| *Control Program:* | **resveratrol** | *Bandwidth:* | **n.a.** |
| *Quantif. Method:* | **TP Licence** | *Dilution Factor:* | **1,0000** |
| *Recording Time:* | **4/12/2015 12:46** | *Sample Weight:* | **1,0000** |
| *Run Time (min):* | **9,89** | *Sample Amount:* | **1,0000** |




| No. | Ret.Time min | Height mAU | Area mAU*min | Asymmetry(EP) | Peak Width min |
|---|---|---|---|---|---|
| 1 | 1,27 | 204,144 | 18,577 | 1,17 | 0,12 |
| 2 | 7,26 | 3,006 | 0,754 | 1,13 | 0,40 |

*Figure 3: Chromatogram of unfiltered Knotweed Rhizome Extract (KRE). Results are from high-performance liquid chromatography with a UV detector set at 306 nm and a 60/40 water:acetonytril mobile phase through a C18 column. We used commercially available resveratrol for calibration.*

## Appendice E

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**CURRICULUM VITAE**

### Formation universitaire & Expérience scientifique:

| | |
|---|---|
| **Actuellement** | **Doctorat en biologie**, sous la direction de Matthieu Chauvat (Pr-HDR) & Estelle Forey (HDR). Sujet : R*elations fonctionnelles entre compartiments épigés et endogés : cas des invasions biologiques végétales*, Université de Rouen, France. Voir *Compétences* ci-dessous. |
| | **Attaché Temporaire d'Enseignement et de Recherche (A.T.E.R.)**, à l'UFR de Sciences & Techniques de l'Université de Rouen Normandie (88h pendant l'année universitaire 2018/2019). TP/TD dispensés en Botanique (systématique, physiologie, sylviculture), Zoologie (systématique), Biostatistiques, Ecologie (communautés), sorties terrain. |
| **2017-2018** | **Moniteur en biologie**, à l'UFR de Sciences & Techniques de l'Université de Rouen Normandie (64h pendant l'année universitaire 2017/2018). TP/TD dispensés en Botanique, Biostatistiques, Ecologie, Ethologie. |
| **2014-2015** | **Master 2 (MSc)** Etude et compréhension de la biodiversité (BIODIV), Université de Rouen, France (B - 2$^{e}$ / 16) |
| | **Stage (6 mois)** *Etude des patrons de diversité fonctionnelle épigée et endogée le long de plusieurs gradients environnementaux*, Laboratoire ECODIV, Université de Rouen, France |
| **2013-2014** | **Master 1 (MSc)** Etude et compréhension de la biodiversité (BIODIV), Université de Rouen, France (AB - 2$^{e}$ / 16) |
| | **Stage (3 mois)** *Etude de l'impact de différentes pratiques agronomiques sur la macrofaune lombricienne du sol : cas du travail du sol et de l'introduction de légumineuses dans les rotations de cultures*, Laboratoire ECODIV, Université de Rouen, France |
| **2009-2013** | **Licence (BSc)** Ecologie et Biologique des Organismes (EBO), Université de Rouen, France (AB - 5$^{e}$ / 52) |
| | **Stage (2 mois)** *Suivi floristique de la restauration d'une zone de dunes suite à la tempête Xynthia*, Réserve Naturelle Nationale de Moëze-Oléron, Ligue de Protection des Oiseaux (LPO), Rochefort, France. |
| **2008** | **Baccalauréat Scientifique**, Lycée Français d'Irlande, Dublin, Irlande |

## Publications :

- Abgrall, C., Chauvat, M., Langlois, E., Hedde, M., Mouillot, D., Salmon, S., ... & Forey, E. (2017). Shifts and linkages of functional diversity between above-and below-ground compartments along a flooding gradient. *Functional Ecology*, 31(2), 350-360.
- Abgrall, C., Chauvat, M., Forey, E. (2018) Invasion by Fallopia japonica alters soil food webs through secondary metabolites. *Soil Biology and Biochemistry*, 127, 100-109
- Abgrall, C, Forey, E., Chauvat, M. (2019) Soil fauna responses to invasive alien plants are determined by trophic groups and habitat structure: a global meta-analysis. *Oikos*.

## Compétences :

| | |
|---|---|
| **Travail de terrain** | Organisation administrative ; Echantillonnage de méso- et macrofaune ; prélèvements de sols (carottes, densité apparent, etc) ; inventaires floristiques (principalement en milieux forestiers et dunaires) ; détermination de surfaces terrières, densités de peuplement, hauteur de fut ; ouverture de canopée (estimation et quantification) |
| **Travail de laboratoire** | *Flore :* mesure de traits en laboratoire (LA, SLA, LDMC, LNC, LCC) ; *Faune :* Extraction de la mésofaune ; identification spécifique des collemboles ; identification ordinale/sub-ordinale des acariens ; identification des trophiques des nématodes. *Microbiologie :* biomasse microbienne (Fumigation-extraction TOC N-POC) ; détermination de la biomasse fongique ; *Sol :* cinétique de la dégradation de la litière, carbone et azote total (CHN), azote organique ($NH_4^+$/$NO_3^-$), pH, calcimètrie, conductimétrie |
| **Analyse de données** | Gestion de données (Access &R) ; Calculs d'indices de diversités taxonomiques et fonctionnelles (α, β, γ) ; Analyses statistiques univariées, multivariées (exploratoire et quantitative), modélisation (LM(M), GLM(M), SEM/Path analysis) et spatiales (sous ArcGIS). |
| **Logiciels utilisés** | R, ArcGIS, qGIS, Access, Mendeley, Office |
| **Langues** | Français (maternel), Anglais (billingue, C2+) |

## Bourses & Financement :

- **Lauréat 2017** d'une bourse DUFRENOY/Crédit Agricole de l'**Académie d'Agriculture de France** (2000€)

## Communications :

- **Séminaire SFR SCALE** (Sciences Appliquées à l'Environnement) en 2016 : **poster affiché** présentation des objectifs de thèse sur l'*Etude des relations entre flore et faune du sol : cas des invasions biologiques végétales*, Université de Rouen, France
- **TEBIS IV – ROUEN 2015** (Traits Ecologiques et Biologiques des Invertébrés du Sol) en 2015 : **communication orale** sur les *Décalages et liens de diversité fonctionnelle entre compartiments épigés et endogés le long d'un gradient d'inondation*, Université de Rouen, France
- **TEBIS V – TOULOUSE 2016** (Traits Ecologiques et Biologiques des Invertébrés du Sol) en 2015 : **communication orale** sur les *Décalages et liens de diversité fonctionnelle entre compartiments épigés et endogés le long d'un gradient d'inondation*, Université de Rouen, France
- **Séminaire SFR SCALE** (Sciences Appliquées à l'Environnement) en 2017 : **poster affiché** *Invasion by Fallopia Japonica alters soil food webs through secondary metabolites*, Université du Havre, France. **Prix du jury du meilleur poster**.
- **Ecology Accross Borders (EAB) 2017** organisé par la British Ecological Society (BES) à Ghent, Belgique : **poster affiché** *Invasion by Fallopia Japonica alters soil food webs through secondary metabolites*.

## Formations spécifiques :

- **Atelier** sur les **méta-analyses en Ecologie** organisé en 2016 dans le cadre du programme de recherche « *Biodiversité, gestion forestière et politiques publiques* » par le GIP ECOFOR

## Expériences professionnelles :

| | |
|---|---|
| **2011-2015** | **Prestataire en restauration événementielle**, *La Fiesta Paëlla*, Société WIN Services, France |
| **2013-2014** | **Médiateur vacataire***, Muséum d'Histoire Naturelle de Rouen*, Mairie de Rouen, France |
| **2011** | **Vacataire archiviste**, *Centre des Archives Diplomatiques du Ministère des Affaires Etrangères*, Nantes, France |

*« Technocrates, c'est les mecs que, quand tu leur poses une question, une fois qu'ils ont fini de répondre, tu comprends plus la question que t'as posée. »*

*- Coluche*

## Abstract

Invasive alien plants are species introduced and naturalized outside of their native distribution range and which have the capacity to maintain and expand their population. Some of these species are considered to be ecosystem transformers by altering their structure, functioning as well as resident animal and plant communities. These induced alterations make some of these species undesirable through their ecological and economical impacts.

The work presented in this thesis aimed at a better understanding of the impact of biological invasions by alien plants. The soil fauna, native vegetation and their substrate, as well as ecosystem functioning, were studied at different spatial scales. Two exotic alien species, invasive in Europe, were considered as biological models for this work: the black locust (*Robinia pseudoacacia*) and the Japanese knotweed (*Reynoutria japonica*).

Firstly, a global meta-analysis demonstrated the positive impact that plant invasions can exert on the abundance of some groups within the soil fauna, notably primary consumers, within different types of habitats (open or closed).

Then, a large-scale study on the black locust revealed the differences that can can occur in the response of forest ecosystems to invasions along a latitudinal gradient. Study sites along this gradient, distributed amog four distinct regions in western Europe, exhibit differences in climate and dominant native vegetation which can alter the impact of the black locust. A detailed study on black locust impact in Normandy demonstrated the impact of *R. pseudoacacia* on native plant and soil fauna communities, as well as some ecosystem functions, in comparison to two native tree species.

Finally, a laboraty experiment demonstrated the impact that allelopathic compounds extracted from Japanese knotweed rhizomes can have on some organisms within the soil fauna. This study showed that some invasive alient plants can influence the soil fauna, and soil food webs, through their secondary metabolism.

This thesis illustrates that simultaneous study of both aboveground and belowground ecosystem compartments at different spatial scales is of interest in the context of biological invasions.

*Keywords :* biological invasions, soil-plant interaction, soil fauna, community ecology, black locust, Japanese knotweed

## Résumé

Les espèces exotiques envahissantes végétales sont des plantes introduites et naturalisées hors de leur aire de répartition native et capables de maintenir et d'accroitre leur population. Certaines sont considérées comme transformatrices de par leur effet sur les écosystèmes : leur structure, leur fonctionnement ainsi que leur communauté végétale et animale. Ces transformations peuvent rendre certaines de ces espèces nuisibles de par leurs impacts écologiques et économiques important.

Les travaux réalisés dans le cadre de cette thèse et présentés ici ont pour objectif d'approfondir les connaissances sur l'impact des invasions biologiques. La faune du sol, la végétation native et leur substrat ainsi que son fonctionnement ont été étudiés à différentes échelles spatiales. Deux espèces exotiques, envahissantes en Europe, ont été considérées comme modèles pour ces travaux : le robinier faux-acacia (*Robinia pseudoacacia*) et la renouée du japon (*Reynoutria japonica*).

Premièrement, une méta-analyse globale a permis de démontrer l'effet positif des invasions biologiques végétales sur l'abondance de certains groupes de la faune du sol, notamment les consommateurs primaires, en fonction de la structure de l'habitat (ouvert ou fermé).

Ensuite, une étude à large échelle sur le robinier faux-acacia a permis d'illustrer les différences qui peuvent exister dans la réponse des écosystèmes forestiers aux invasions le long d'un gradient latitudinal. Ce gradient, composé de quatres régions distinctes en Europe de l'Ouest présente des différences de climat et de végétation dominante, ces différences modifiant l'impact du robinier faux-acacia. Une étude apponfondie sur le robinier faux-acacia en Normandie a permis de mieux comprendre l'effet du robinier faux-acacia sur les communautés animales et végétales ainsi que sur le fonctionnement des écosystèmes par comparaison avec deux essences natives dominantes.

Finalement, une manipulation expérimentale en laboratoire a démontré l'impact des composés allélopathiques de la renouée du Japon sur une partie de la faune du sol. Cette étude a montré que certaines espèces exotiques envahissantes sont susceptibles d'influencer la faune, et les réseaux trophiques, du sol par leur métabolisme secondaire.

Ces travaux illustrent l'intérêt, dans le contexte des invasions biologiques végétales, de l'étude simultanée des compartiments aériens et soutterrains à différentes échelles spatiales.



*Mots-clés :* invasions biologiques, interactions sol-plantes, faune du sol, écologie des communautés, robinier faux-acacia, renouée du Japon