



interactions plantes - macroinvertébrés du sol dans les forêts européennes : structuration des communautés et interactions avec la microfaune en contexte de changement climatique

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

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École doctorale GAIA

Centre d'Ecologie Fonctionnelle et Evolutive

**Interactions plantes - macroinvertébrés du sol dans les
forêts européennes: structuration des communautés et
interactions avec la microfaune en contexte de
changement climatique.**

Présentée par Pierre GANAULT

Le 8 Décembre 2020

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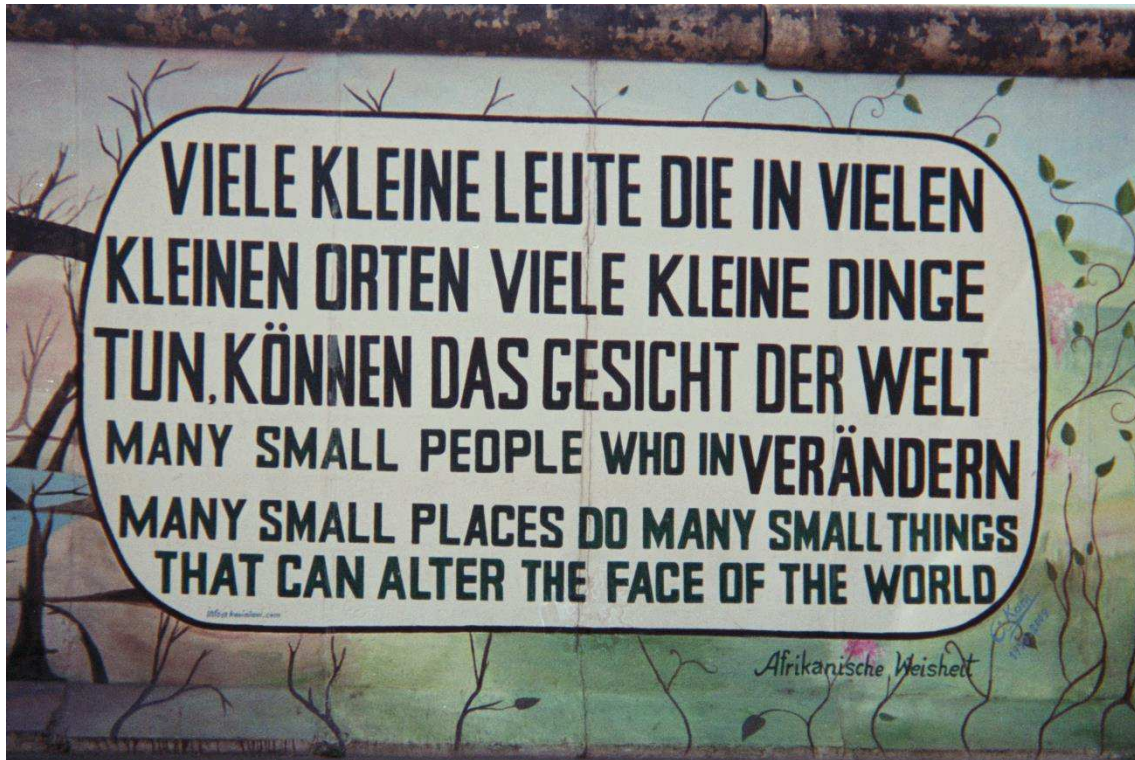
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UNIVERSITÉ
DE MONTPELLIER



« Une multitude de petites personnes qui dans une multitude de petits lieux font une multitude de petites choses qui peuvent changer le monde »

Eduardo Goleano

Peinture murale sur le mur de Berlin

RESUME

Les communautés du sol sont extrêmement diverses et comprendre leur distribution et leur structure est un défi scientifique car elles sont influencées par de nombreux facteurs abiotiques et biotiques. Etudier les organismes du sol est cependant primordial car ils interviennent dans de nombreux processus du sol, tels que la décomposition des matières organiques et le recyclage des éléments nutritifs. Cependant, nos connaissances des processus fins impliqués dans la structuration de leurs communautés et dans la façon dont ils influencent le fonctionnement du sol restent souvent limitées. Pour combler ces lacunes, ma thèse de doctorat se concentre dans un premier temps sur les facteurs abiotiques et biotiques qui façonnent les communautés de macroinvertébrés des sols forestiers tempérés, avant d'étudier leur rôle dans la décomposition de la litière et la manière dont ils influencent les autres organismes du sol dans le contexte des changements climatiques. Le premier volet de la thèse (chapitres 1 et 2) est une approche in situ, où les communautés de macrofaune ont été étudiées dans des forêts de composition et de diversité spécifique en arbres variables le long d'un gradient latitudinal européen (incluant des sites en Italie, Roumanie, Pologne et Finlande). Le premier chapitre étudie l'importance relative de la diversité des arbres, de leur type fonctionnel et de l'environnement physique dans la structuration des assemblages de macrofaune prédatrice et sapro-géophage. Dans un second chapitre, je me suis plus particulièrement intéressé aux communautés de coléoptères carabiques en appliquant une approche basée sur les traits fonctionnels à l'aide de mesure individuelles et de données tirées de la littérature. L'objectif étant de décrire comment l'environnement forestier et les ressources alimentaires influencent la structure fonctionnelle des communautés de ces insectes prédateurs. Le deuxième volet de la thèse développe des approches expérimentales et se concentre sur l'importance fonctionnelle de la macrofaune sapro-géophage, et notamment les interactions qu'elle entretient avec les plantes d'une part (chapitre 3) et d'autres organismes du sol tels que les nématodes d'autre part (chapitre 4). Les préférences alimentaires de six espèces de macro-arthropodes sapro-géophages communément rencontrées dans les forêts européennes sont décrites dans un premier temps et discutées au regard des caractéristiques physiques, chimiques, et morphologiques des litières. Les conséquences de ces préférences alimentaires sur les propriétés des boulettes fécales produites par ces invertébrés d'une part, et leurs implications pour la décomposition des litières d'autre part sont discutées. Enfin, dans une expérience contrôlée en mésocosme, nous avons étudié la réaction des communautés de nématodes à une sécheresse simulée et la manière dont la diversité fonctionnelle de la macrofaune saprophage peut limiter les effets délétères de la sécheresse. L'importance de la biodiversité du sol, à différents niveaux trophiques et dans ses dimensions taxonomiques et fonctionnelles, est discutée du point de vue du fonctionnement du sol et des écosystèmes forestiers tempérés. Les résultats sont ensuite discutés afin d'identifier des pratiques de gestion sylvicoles permettant de préserver la biodiversité des sols et les fonctions qu'elle assure à l'échelle de l'écosystème, en dépit des changements globaux.

ABSTRACT

Soil communities are extremely diverse and understanding the drivers of their distribution and structure is challenged by the multitude of abiotic and biotic factors that might influence them. However, studying soil organisms is essential because they are involved in many soil processes, such as organic matter decomposition and nutrient cycling. However, our knowledge of the fine processes involved in the structuring of their communities and how they influence soil functioning is often limited. To fill these gaps, my PhD thesis first focuses on the abiotic and biotic factors shaping macroinvertebrate communities in temperate forest soils, before studying their role in litter decomposition and how they influence other soil organisms in the context of climate changes. The first part of the thesis (chapters 1 and 2) is an in situ approach, where macrofauna communities were studied in forests of varying tree composition and specific diversity along a European latitudinal gradient (including sites in Italy, Romania, Poland and Finland). The first chapter examines the relative importance of tree diversity, tree functional type and physical environment for predatory and sapro-geophagous macrofauna communities. In a second chapter, I focused on carabid beetle assemblages by applying a functional trait-based approach using individual measurements and data obtained from the literature. The objective was to describe how the forest environment and the characteristics of their food resource influence the functional structure of their communities. The second part of the thesis develops experimental approaches and focuses on the functional importance of the sapro-geophagous macrofauna, and in particular the interactions it maintains with plants on the one hand (chapter 3) and with other soil organisms such as nematodes on the other (chapter 4). The feeding preferences of six species of saprophagous macroarthropods commonly found in European forests are first described and discussed with regard to the physical, chemical and morphological trait-based characteristics of the litter. The consequences of these feeding preferences on the properties of the faecal pellets produced by these invertebrates on the one hand, and their implications for the decomposition of litter on the other, are discussed. Finally, in a controlled mesocosm experiment, we studied the response of nematode communities to a simulated drought and how the functional diversity of the sapro-geophagous macrofauna can limit the deleterious effects of drought. The importance of soil biodiversity, at different trophic levels and in its taxonomic and functional dimensions, is discussed from the point of view of soil functioning and temperate forest ecosystems. The results are then discussed in order to identify silvicultural management practices that preserve both soil biodiversity and the functions it performs at the ecosystem level, despite global changes.

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Introduction

La Terre abrite une incroyable diversité d'organismes que l'être humain étudie et classifie depuis l'Antiquité. Depuis les travaux de Carl von Linné, Charles Darwin et Willi Hennig, la comparaison des caractères anatomiques, physiologiques, puis moléculaires des organismes a permis la classification cladistique du Vivant (Lecointre et al. 2016). Grâce au développement et à l'amélioration des techniques pour observer et décrire les organismes, nous estimons aujourd'hui à 8,7 millions le nombre d'espèces eucaryotes sur Terre, mais n'aurions décrit que 1,5 millions (Mora et al. 2011). Cette multitude d'organismes vivants interagit avec son environnement physique et régule les grands cycles biogéochimiques et le fonctionnement des écosystèmes (Tansley 1935). La biodiversité est ainsi à la base de nombreux processus écosystémiques dont dépend la population humaine à la fois pour son alimentation, son bien-être, et le maintien de conditions vivables sur Terre (Cardinale et al. 2012; Marselle et al. 2019). Malgré son importance pour l'être humain et sa valeur intrinsèque (Naess 1998), la biodiversité subit un déclin du à la dégradation des habitats, la surexploitation de certaines espèces, les pollutions et les changements climatiques liés aux activités humaines (Cardinale et al. 2012; Johnson et al. 2017). A titre d'exemples, il a récemment été estimé que l'abondance et la biomasse des espèces de mammifères avaient chuté de 82% (Figure 1.1; Díaz et al. 2019) et que la biomasse d'insectes volants dans les aires protégées allemandes avait diminuée de 75% en 27 ans (Hallmann et al. 2017). Les études sur l'érosion de la biodiversité, tout comme les mesures de conservation, négligent cependant souvent une part considérable de la biodiversité, qui se trouve dans les sols (Decaëns et al. 2006). Malgré leur rôle fondamental dans de nombreux processus écosystémiques et leur immense diversité, les organismes du sol restent en effet trop peu étudiés et la réponse de ces communautés aux changements globaux reste encore méconnue (Wall et al. 2012; Veresoglou 2015; Eisenhauer et al. 2019a).

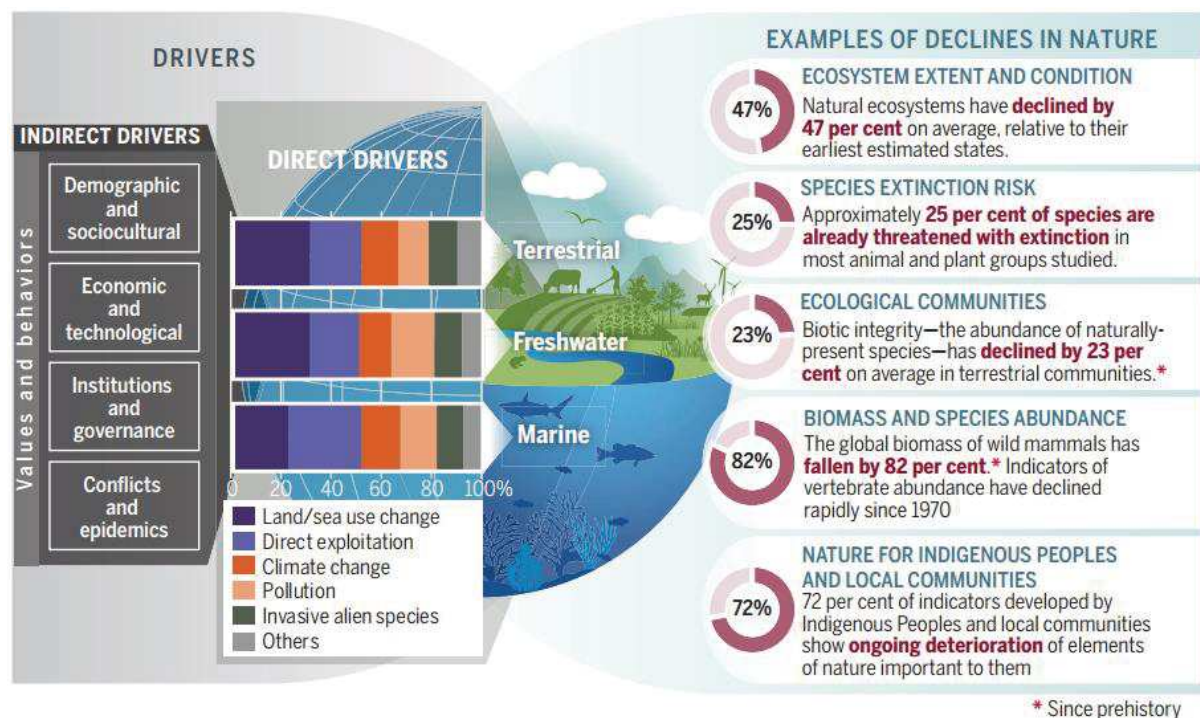


Figure 1.1. Exemples de déclin global dans les écosystèmes qui ont été et sont causés par des facteurs directs et indirects. Chaque facteur direct (changement d'utilisation des eaux/terres, exploitation directe, changements climatiques, pollution, espèces invasives) représente l'agrégation de nombreuses conséquences de secteurs comme l'agriculture, la pêche, la sylviculture, l'extraction minière, l'urbanisation, ou le transport. Les facteurs directs résultent d'une multitude de causes sociétales : démographie, culture, économie, technologie, gouvernance, épidémie. Ce sont les causes indirectes sous-tendues par les valeurs sociétales et comportementales. Les bandes de couleurs représentent l'impact relatif global des facteurs directs sur les écosystèmes terrestres, d'eau douce, et marins, estimé à partir d'une synthèse de littérature d'étude publiées depuis 2005. Extrait de Díaz et al. (2019).

1.1. La biodiversité du sol

1.1.1. Diversité taxonomique

Les organismes du sol regroupent toute espèce dont au moins l'un des stades de vie complet et actif se déroule à la surface et/ou dans le sol (Gobat et al. 2010). Ils représenteraient près de 25% des 1,5 millions d'espèces décrites globalement à ce jour (Decaëns et al. 2006), et s'établissent en communautés très denses, mais aussi hétérogènes spatialement, rendant leur échantillonnage exhaustif très difficile, voire impossible, d'autant plus que la majorité de ces organismes sont très petite taille (Decaëns 2010). Sur la base de leur taille (diamètre ou longueur), il est possible de distinguer cinq grands groupes (Swift et al. 1979) : les micro-organismes (bactéries et champignons), la microfaune (nématodes, rotifères...), la mésofaune (collembolles, acariens...), la macrofaune (vers de terre, coléoptères, diplopodes, isopodes...), et la mégafaune (invertébrés géants, mammifères et amphibiens fouisseurs) (Figure 1.2).

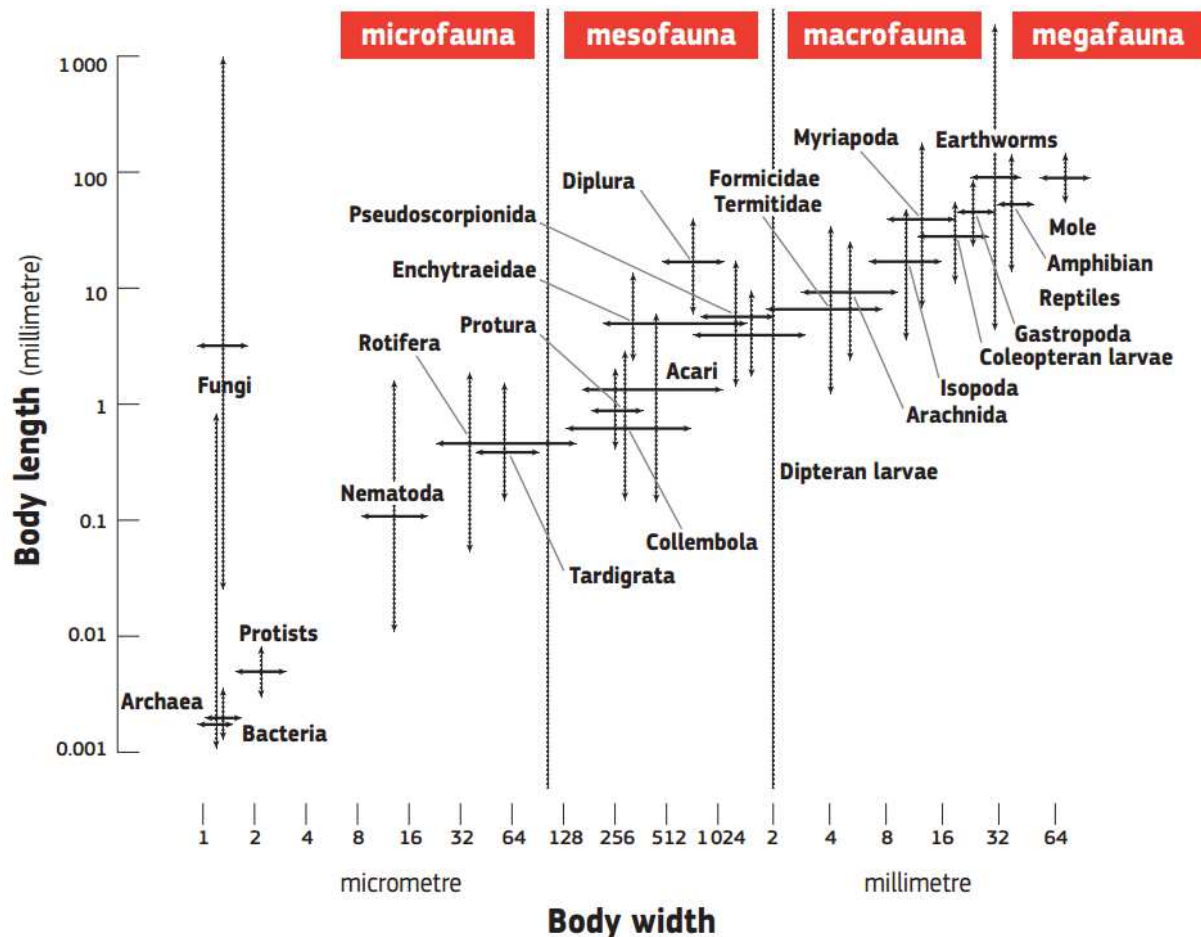


Figure 1.2. Longueur et largeur de grands groupes d'organismes du sol, adapté de Swift et al. (1979) par Orgiazzi et al. (2016).

Malgré cette formidable diversité, l'intérêt que suscitent ces organismes auprès du grand public et de la communauté scientifique est bien moindre que pour des taxons équivalents n'appartenant pas à la faune endogée, faisant de la biodiversité des sols la « dernière frontière biotique » découverte après les abysses océaniques et les canopées des forêts tropicales humides (André et al. 1994). Il existe en conséquence un très important déficit de connaissances de la majorité des organismes du sol, tant sur le plan taxonomique que de leur distribution. Ces deux limites sont connues sont le nom de déficit Linnéen (beaucoup d'espèce n'ont pas été formellement décrites) et déficit Wallacéen (nous ignorons encore beaucoup des aires de distribution de ces espèces) (Whittaker et al. 2005). Le déficit taxonomique est par exemple en moyenne de 76% pour les invertébrés (i.e. les trois quarts des individus d'un échantillon ne peuvent être assignés avec certitude à une espèce) et est inversement proportionnel à la taille des organismes : les taxons les plus petits sont les moins bien connus avec 96% de déficit taxonomique pour les bactéries et champignons (Figure 1.3; André et al. 2002; Decaëns 2010).

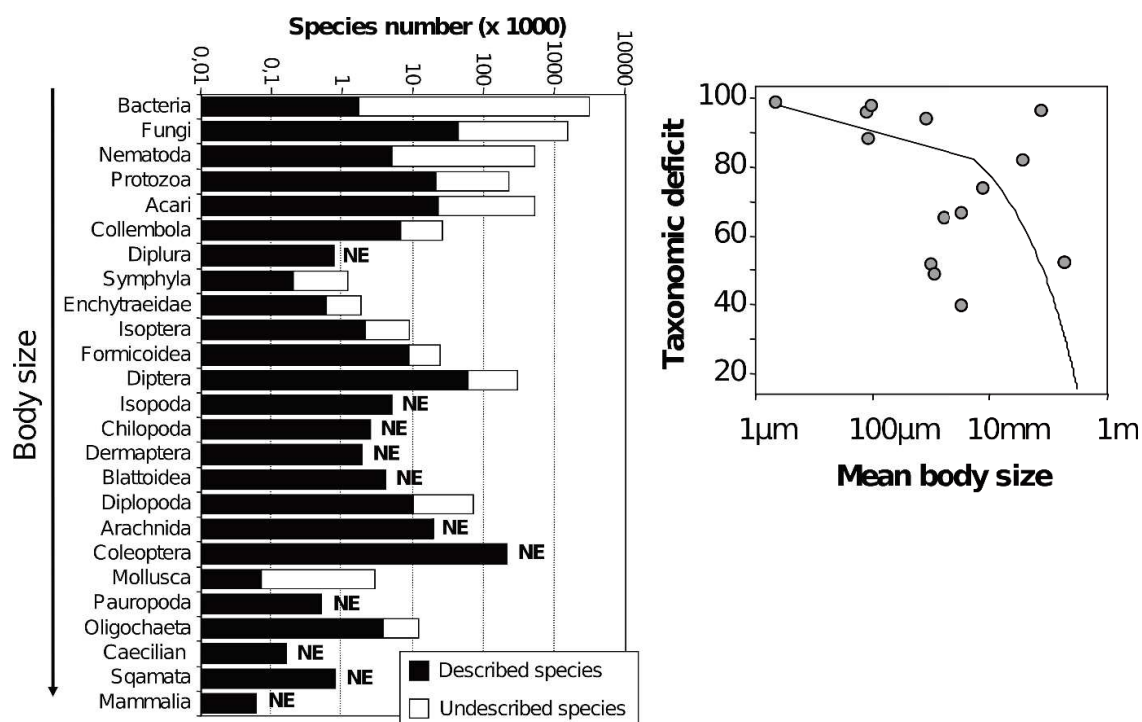


Figure 1.3 – Nombre d'espèce (décrites et non décrites estimées) par groupe taxonomique classé par ordre de taille (gauche) et déficit taxonomique en fonction de la taille moyenne (droite). Extrait de Decaëns (2010).

Toutefois, même les taxons du sol de grande taille comme les vers de terre révèlent une diversité insoupçonnée dans les régions peu étudiées et/ou lorsqu'on les étudie à l'aide des nouvelles techniques moléculaires d'identification (King et al. 2008; Decaëns et al. 2016; Porco et al. 2018). Le groupe de la macrofaune peut effectivement contenir des espèces cryptiques, c'est-à-dire indissociables à partir des critères morpho-anatomiques mais qui diffèrent suffisamment dans leur génome pour être considérées comme des espèces différentes (Blaxter et al. 2005). Hormis pour les vers de terre et les fourmis, il existe moins d'études sur la distribution des espèces de groupes de macrofaune que sur les microorganismes ou les nématodes (Guerra et al. 2020). Ce groupe est pourtant au cœur du fonctionnement du sol, et interagit avec les autres organismes du sol et les plantes dans la réalisation de nombreux services écosystémiques (Lavelle and Spain 2001; Lavelle et al. 2006; Wall et al. 2012).

1.1.2. Diversité de trait

Cette diversité taxonomique de la macrofaune s'accompagne d'une grande diversité de caractéristiques, ou traits, morphologiques, physiologiques, phénologiques, et comportementales mesurables à l'échelle de l'individu (Pey et al. 2014b). Ces caractères

peuvent être reliés à la façon dont une espèce répond aux conditions environnementales (trait de réponse), exploite son environnement (trait d'effet), ou interagit avec d'autres espèces (trait d'interaction) (Moretti et al. 2013). On emploie la terminologie « trait fonctionnel » si ces caractères influencent directement la performance et donc la valeur sélective de l'individu (Violle et al. 2007). Le concept de trait fonctionnel initialement développé sur les communautés de plantes a permis de mieux comprendre comment différents filtres environnementaux sélectionnent des espèces sur la base de leur traits de réponses, résultant en une communauté présentant certains traits d'effet qui influenceront les processus écosystémiques (Figure 1.3 A; Lavorel and Garnier 2002). L'application de ce cadre conceptuel à la faune du sol a nécessité l'adaptation de la terminologie (Pey et al. 2014a) et la construction de bases de donnée pour répertorier les connaissances scientifiques sur les traits et l'occurrence des organismes du sol (e.g. BETSI, Pey et al. 2014a; and EDAPHOBASE, Burkhardt et al. 2014). En plus de mesures directes sur les organismes, à partir de la littérature et d'ouvrages d'identification, il est possible de rassembler les valeurs de taille des organismes (longueur, masse fraîche ou sèche, largeur), les régimes alimentaires (zoophage, saprophage, généraliste, rhizophage, graminivore), les préférences d'habitat (spécialiste ou généraliste), les caractéristiques des appendices locomoteurs (ailes fonctionnelles, longueur des pattes), ou encore les périodes et stratégie de reproduction. L'utilisation des traits fonctionnels pour décrire les communautés d'organismes du sol est très récente comparée à son historique en écologie végétale, et transposer les outils développés sur les plantes aux animaux est une question complexe d'un point de vue méthodologique. Un effort important est réalisé pour développer des méthodes standardisées de mesures des traits fonctionnels pertinents pour décrire la réponse ou l'effet des espèces animales édaphiques (Moretti et al. 2017). Toutefois, la majorité des études sur les arthropodes terrestres justifient de manière insuffisante la sélection des traits des organismes, et les liens entre les traits et les fonctions étudiées restent faibles, voire non démontrés expérimentalement (Brousseau et al. 2018b; Wong et al. 2019). En conséquence, pour améliorer le pouvoir prédictif des études basées sur les traits fonctionnels des arthropodes terrestres, ces derniers auteurs proposent de suivre une démarche séquentielle permettant de définir simultanément les liens entre les facteurs/filtres environnementaux et les traits de réponse, ainsi qu'entre les traits d'effet et les processus écosystémiques que les espèces peuvent influencer (Figure 1.4).

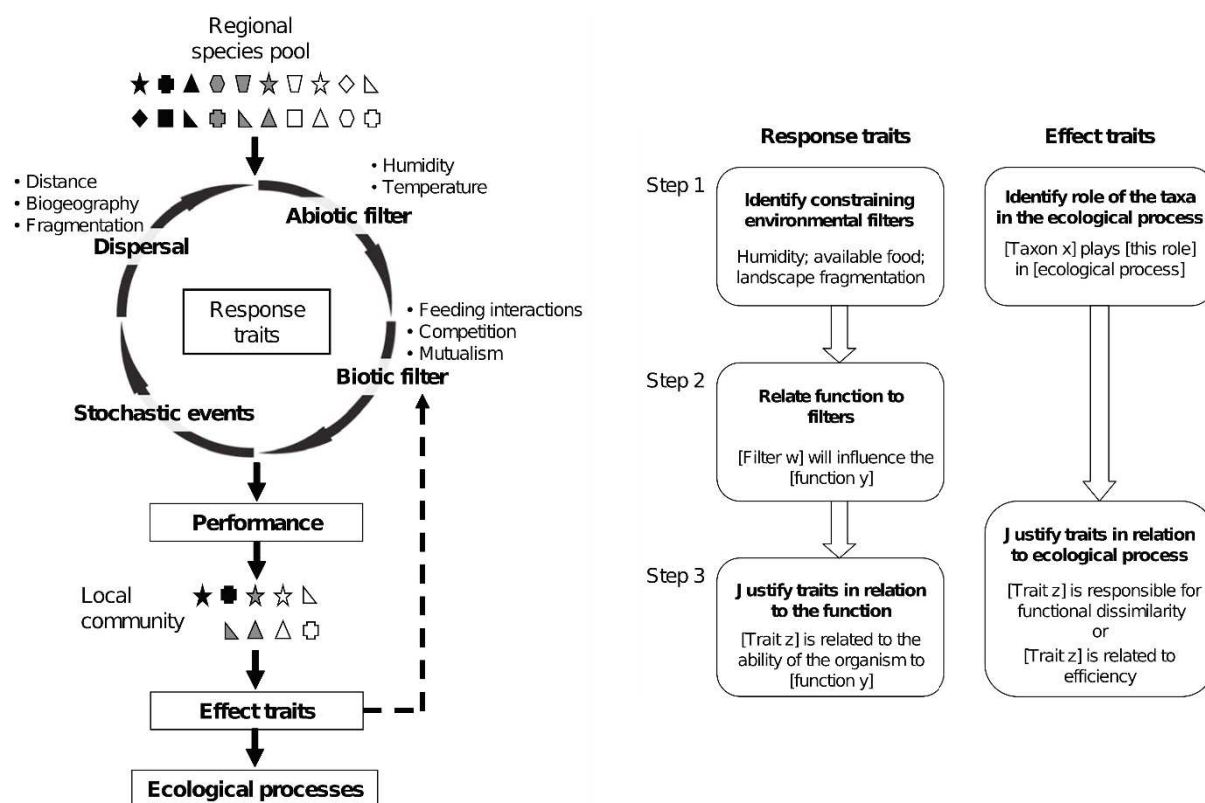


Figure 1.4 – A) Représentation des différents filtres qui aboutissent à un assemblage local d'espèces et de traits particuliers à partir d'un pool régional. Chronologiquement, le pool d'espèce régional est défini par l'évolution, la biogéographie et les mécanismes de migration/dispersion entre différentes régions. L'assemblage local est ensuite la résultante de différents filtres qui agissent simultanément et sélectionnent les espèces sur la base de leurs traits de réponse. La communauté locale présente un ensemble particulier de traits d'effet qui affecteront l'environnement dans une boucle de rétroaction (flèche pointillée). **B)** Protocole séquentiel pour définir clairement les hypothèses dans les études sur les traits de réponse et d'effet appliqués aux arthropodes. Extrait de Brousseau et al. (2018).

1.1.3. Diversité de rôle dans l'écosystème

Une façon d'appréhender la grande diversité taxonomique et morphologique des organismes du sol pour étudier leur effet sur l'écosystème a été de regrouper les espèces en fonction de différents caractères partagés. Classer les organismes par leur taille comme énoncé précédemment (voir 1.1; Swift et al. 1979) reste une pratique largement répandue et pertinente pour savoir à quelle échelle spatiale un individu répond et influence son environnement, bien que certaines espèces d'un même groupe taxonomique, ou certains individus d'une même espèce mais à différents stades de développement puissent appartenir à différentes classes de taille. Les groupes peuvent également être des classifications écomorphiques utilisant à la fois des caractères morphologiques et écologiques et sont souvent utilisées ensuite en tant que groupe fonctionnel, à qui on attribue un ensemble plus

ou moins définit de fonction. Cette classification a été utilisée pour les collemboles (épédaphique, hémi-édaphique ou eu-édaphique ; Gisin 1943; Potapov et al. 2016); et les vers de terre (épigés, endogés et anéciques ; Bouché 1972; Bottinelli et al. 2020). Une troisième méthode est de classer les organismes en fonction de leur régime trophique (phytophage, rhizophage, mycophage, généralistes, prédateurs, saprophages, géophages... Gobat et al. 2010). Cette distinction par groupe trophique peut être utilisée pour différencier des grands groupes taxonomiques (isopodes saprophages) et peuvent être davantage développés pour les groupes présentant de nombreux régimes trophiques (Coléoptères Carabidae et Staphylinidae). Certaines autres classifications se basent sur la stratégie de vie entre *r* (cycle de vie court, petite taille, haute fécondité) and *K* (cycle de vie long, grande taille, faible fécondité). Cette classification a été largement utilisée pour les nématodes (Bongers and Bongers 1998). Enfin, des groupes fonctionnels peuvent également être construits en rassemblant les taxons qui soit répondent de manière similaire à différents gradients environnementaux, soit qui influencent leur environnement de façon similaire (Wilson 1999). Cette approche fonctionnelle permet également de distinguer les transformateurs de litière qui dégradent la litière en boulettes fécales qui peuvent favoriser l'activité microbienne, des ingénieurs de l'écosystème qui modifient leur environnement physique par la création de structures stables (déjections, galeries) et qui interagissent directement avec les bactéries dans leur tube digestif (Jones et al. 1994; Lavelle 2002).

1.1.3.1. Rôle dans la décomposition de la matière organique

La décomposition est l'ensemble des processus de lessivage, fragmentation et minéralisation de la matière organique morte, notamment des litières végétales (Swift et al. 1979). Une partie importante de ce processus est due au climat, aux changements de température et de précipitation, mais surtout à l'activité des microorganismes dont les exo-enzymes digestives hydrolysent et minéralisent les constituants de la litière (Berg and McClaugherty 2008). Conjointement, la macrofaune saprophage (certains vers de terre, isopodes, diplopodes, larves de certaines espèces de diptère) et la mésofaune fungivore (collembole, certains acariens) consomment la litière et la microflore qui se développe à sa surface (Lavelle and Spain 2001). Ces organismes fragmentent les feuilles entières en plus petites particules qui sont agglomérées dans les boulettes fécales dont la composition chimique et les propriétés

physiques sont différentes des caractéristiques initiales de la litière (David 2014a). Cette matière organique est ensuite redistribuée verticalement et horizontalement dans le sol, changeant sa disponibilité pour les microorganismes immobiles (**Figure 1.5**) (Anderson 1988a; Frouz 2018). Certains vers, qui se nourrissent de litière et l'enfouissent dans le sol sont particulièrement importants dans cette redistribution de la matière organique dans le sol. Ainsi, le rôle de la macrofaune dans la décomposition a été étudié en expérimentations en conditions contrôlées ainsi qu'*in situ*, en utilisant des sachets de litières dont la largeur des mailles permet ou non l'accès à la litière à la macrofaune. Ces études ont démontré l'importance de l'activité de cette faune pour la perte en masse des litières dans des biomes très contrastés (Handa et al. 2014). Leur effet est toutefois plus important dans les forêts décidues tempérées et lorsque la litière est de qualité chimique intermédiaire ou basse, c'est-à-dire avec un ratio carbone/azote > 20 (Frouz et al. 2015). Contrairement à notre ancienne vision (van der Drift 1951), les déjections de ces organismes présentent à moyen et long terme une minéralisation du carbone plus faible que celle de la litière initiale, et sont davantage des structures de stabilisation du carbone (David 2014a). A l'inverse, l'excrétion (production de différentes formes d'azote dans les déjections et urines) de la macrofaune, et le ratio C/N plus élevé des boulettes fécales semblent favoriser la minéralisation de l'azote (Joly et al. 2018).

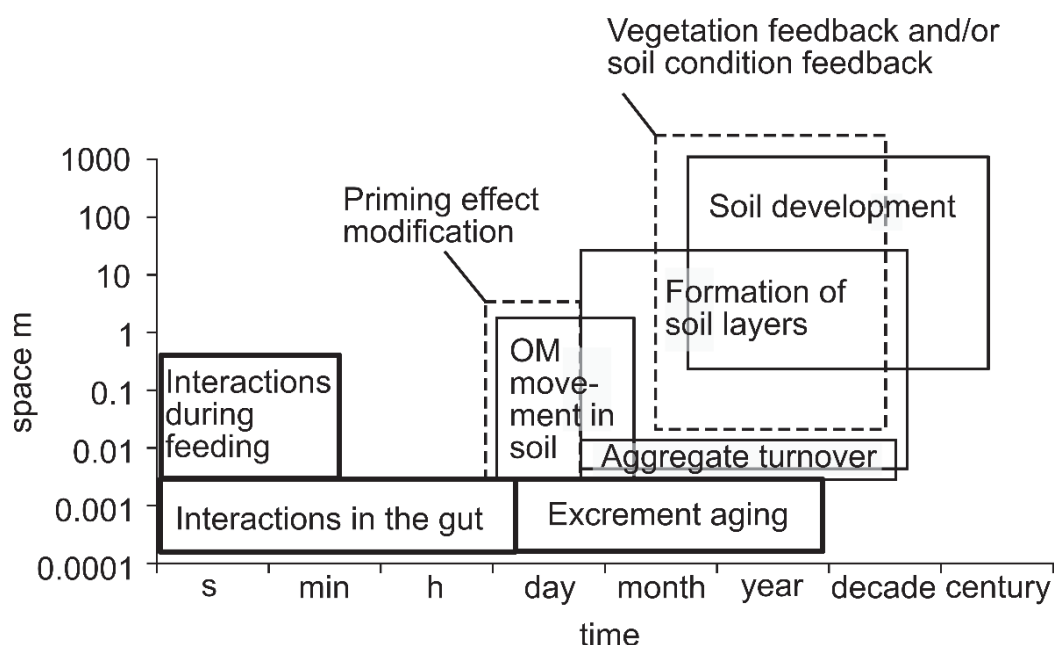


Figure 1.5 – Représentation graphique de l'échelle spatio-temporelle auxquelles se réalisent les processus du sol influencé directement (cadre épais) ou indirectement (cadre fin) par la macrofaune du sol. Redessiné à partir de Frouz (2018).

1.1.3.2. *Structuration du sol et échanges gazeux et hydriques*

La structuration du sol, sa porosité et donc son aération et les transports d'eau sont hautement influencés par l'activité de la faune endogée, qui se déplace dans les différents horizons du sol. Les vers de terre sont les organismes les plus importants à cet égard dans les écosystèmes tempérés. Grâce à leur puissante musculature et leurs soies, ils se déplacent par péristaltisme verticalement et/ou horizontalement et créent des galeries permanentes ou transitoires qu'ils peuvent obstruer pour certaines espèces avec leurs déjections (Lavelle and Spain 2001). De plus, les déjections des vers (turricules) sont des agrégats argilo-humiques de taille généralement centimétrique et physiquement plus stables que les agrégats moyens du sol (Edwards 2004). L'effet d'une espèce de vers sur les propriétés physiques du sol et les flux d'air et d'eau qui s'y produisent dépend du comportement d'enfouissement des vers, que l'on a l'habitude de classer en trois catégories : les vers épigés, anéciques, et endogés (Bouché 1972; Bottinelli et al. 2020a). Les vers épigés restent en surface et ne créent pas de galeries, les vers anéciques creusent des galeries verticales continues (semi)permanentes pouvant connecter la surface avec les horizons profonds du sol, et les vers endogés creusent de nombreuses galeries horizontales, plus étroites et discontinues car souvent rebouchées par leurs déjections (Figure 1.6). Au sein d'une même catégorie, chaque espèce a un comportement d'enfouissement différent et affecte différemment les échanges gazeux et hydriques (Capowiez et al. 2015). De cette activité de bioturbation résulte en général une infiltration plus importante de l'eau ainsi qu'une meilleure aération du sol (Shipitalo and Le Bayon 2004), deux mécanismes contribuant à l'effet positif des vers de terre sur l'activité microbienne et la croissance de plantes (Scheu 2003; Blouin et al. 2013). Bien que les vers de terre (et les racines) soient les principaux acteurs de la structuration et macroporosité des sols, d'autres organismes sont capables de créer des galeries. En effet, une grande partie des macroinvertébrés comme les Coléoptères pondent dans le sol, et leur larves évoluent dans les premiers centimètres du sol (Lindroth 1985; Luff 1998), tandis que les isopodes et diplopodes peuvent s'enterrer pour trouver des microhabitats humides voire entrer en diapause estivale (David and Handa 2010). De plus l'incorporation des boulettes fécales de la macrofaune améliore également la microporosité du sol et la création de microhabitats favorables à l'activité biologique (Anderson 1988a; Coulis et al. 2016a)

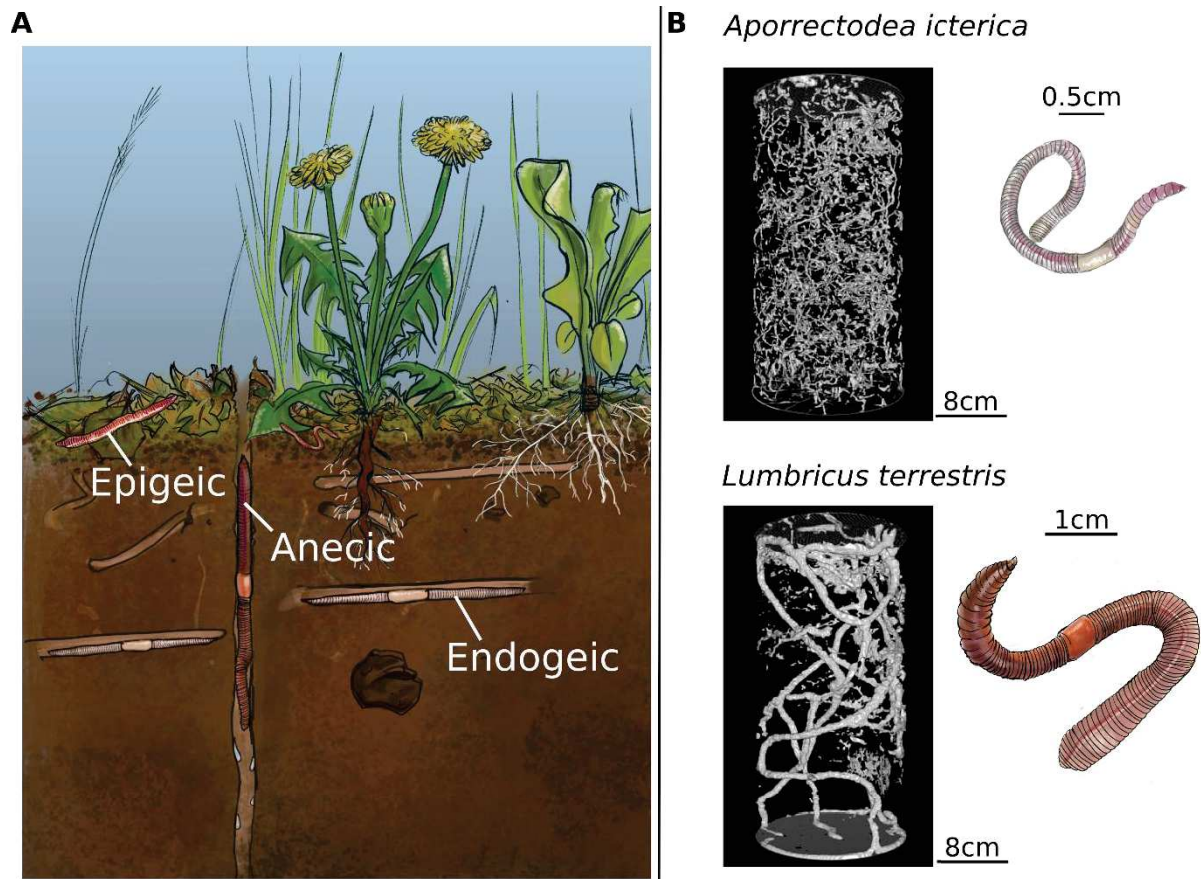


Figure 1.6 - A. Illustration des différentes catégories écologiques et **B.** reconstruction des galeries de deux espèces par tomographie au rayon X (Ganault et al., soumis). Illustrations par Morgane Ganault Arrieta (www.lesbullesdemo.com).

1.1.3.3. Régulations trophiques par les prédateurs

La présence de prédateurs peut fortement influencer le fonctionnement des écosystèmes lorsqu'ils exercent une forte pression de prédation sur les organismes des niveaux trophiques inférieurs impliqués dans transformation de la matière organique (détritvore ou herbivore). Premièrement, la consommation directe d'une proie, sa digestion et la production de déjections libèrent une partie des nutriments contenus dans les tissus de la proie, souvent au bénéfice des plantes. On observe ainsi une remobilisation importante des nutriments lorsque des nématodes microbivores se nourrissent de bactéries ou champignons ou que des nématodes prédateurs et omnivores se nourrissent d'autres nématodes (Bonkowski et al. 2009). De plus, la simple présence de prédateurs entraîne un changement de comportement de la proie qui peut cesser son activité de nutrition pour se cacher, limitant ainsi le rôle de la proie en tant que consommateur (Schmitz et al. 2004). Le stress induit par la présence de prédateurs peut également augmenter la transformation de protéines en sucre, changeant ainsi la stœchiométrie des tissus de la proie avec une augmentation du rapport C/N qui peut

par la suite négativement affecter la décomposition (Hawlena et al. 2012). Finalement, les prédateurs jouent un rôle prépondérant dans la régulation des populations de proies et peuvent fortement modifier la composition des communautés de proies. Cette aptitude a été fortement étudiée car elle représente un des moyens de lutte biologique contre les ravageurs des (sylvi)cultures (Weseloh 1985; Letourneau et al. 2009). L'effet des prédateurs sur ses proies et les processus écosystémiques est mieux prédit en prenant en compte les traits de prédateurs et des proies. Par exemple, la taille des espèces au sein des assemblages de prédateurs permet de mieux prédire le type et le nombre de proies qui seront consommées (Rusch et al. 2015). De même, le changement de comportement (se dissimuler plutôt que se nourrir) d'une proie herbivore dépend de sa perception du risque de prédation qu'elle perçoit et qui dépend des différentes stratégies de chasse utilisées par les prédateurs. Notamment, les araignées qui chassent activement en se déplaçant produisent un risque de prédation plus aléatoire et moins contraignant que les araignées à stratégie « sit-and-wait » qui, étant toujours présentes à un endroit, exercent une pression de prédation forte et constante que les proies vont chercher à éviter (Schmitz 2008).

1.1.3.4. Interactions biotiques : les relations macrofaune-microfaune

D'autres organismes du sol ayant un rôle prépondérant dans le fonctionnement des communautés microbiennes, les nématodes, sont également sensibles aux modifications du sol induites par la macrofaune. Ce groupe très diversifié d'organismes regroupe près 40.000 espèces vivant dans des milieux très différents et parfois extrêmes grâce à leur capacité à résister aux sécheresses et autres perturbations en arrêtant leur activité biologique en entrant en anhydrobiose (Yeates 1979). Ces organismes ont des régimes trophiques très variés (bactérovores, fungivores, omnivores, prédateurs, parasites de plantes et d'animaux) et influencent ainsi fortement le recyclage des nutriments dans les sols par la remobilisation des nutriments des communautés microbiennes, favorisant par ce biais la croissance des plantes (Bongers and Bongers 1998; Bonkowski et al. 2009). La modification des communautés microbiennes par l'activité de la macrofaune est également susceptible d'influencer les communautés de nématodes par effet bottom-up. De plus, les nématodes sont des organismes aquatiques qui vivent et se déplacent dans l'eau interstitielle du sol et ils sont donc sensibles aux modifications des flux d'eau induites par les ingénieurs du sol tels que les vers

de terre (Dionísio et al. 2018). Les interactions entre microfaune et macrofaune sont toutefois très peu étudiées, notamment l'effet des macroarthropodes saprophages (Bastow 2011). Dans les sols, l'ensemble des organismes interagissent, à l'instar du micro réseau trophique des nématodes, et déterminent les processus écosystémiques. L'intégration des interactions multitrophiques et de la diversité à différents niveaux trophiques permettra de mieux comprendre les rôles des organismes du sol dans (Eisenhauer et al. 2019b).

1.2. Structuration des communautés du sol en forêt

L'étude de la structuration des communautés de macrofaune du sol nécessite de définir précisément l'échelle d'observation car celle-ci détermine la nature des facteurs de contrôle ainsi que la façon dont il vont filtrer les traits des espèces édaphiques et déterminer la composition des assemblages présents dans un habitat et à un moment donné (Ettema and Wardle 2002; Figure 1.7; Berg 2012). A une grande échelle (continentale, sur plusieurs kilomètres), le climat, le type de sol ou encore la quantité d'énergie solaire disponible constituent les forçages environnementaux les plus importants. A cette échelle l'occurrence d'une espèce est principalement déterminée par sa capacité de dispersion ainsi que sa niche climatique. A l'inverse, à une échelle plus fine (quelques décimètres) l'agrégation du sol ou encore la distribution verticale et temporelle de l'eau et des nutriments sont prépondérants. A ce niveau s'applique un filtre important sur les capacités de résistance des espèces aux fluctuations environnementales stressantes (par ex. cycles de séchage-réhumectation). Dans cette thèse, je me suis d'abord intéressé à une échelle intermédiaire (parcelle, quelques mètres), où l'effet d'organismes individuels (plante, faune), le microclimat et la disponibilité en microhabitats sont prépondérants. A cette échelle, les communautés de macrofaune se structurent en fonction de leur habilité à utiliser leur ressource et habitat, et éviter la prédation. Plusieurs parcelles furent étudiées, regroupées dans quatre sites étalés le long d'un gradient permettant de tester la robustesse des relations environnement – macrofaune du sol à l'échelle de la parcelle dans différents contextes pédoclimatique à une échelle plus large. Les interactions à fine échelle (quelques cm-dm) entre macrofaune et microfaune furent également étudiées en conditions contrôlées.

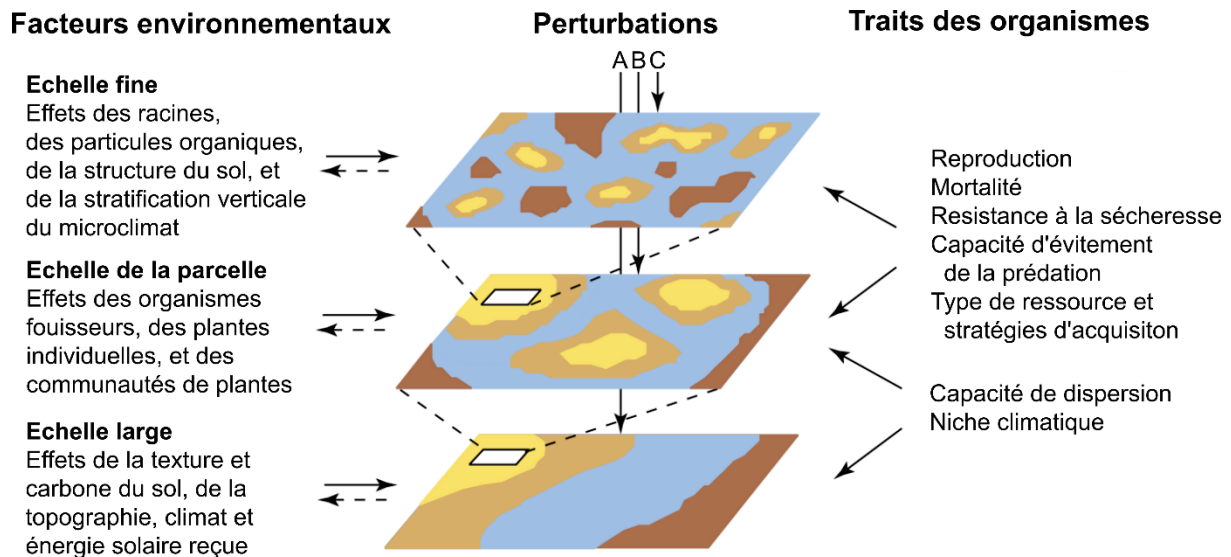


Figure 1.7 – Distribution emboîtée des communautés du sol à différentes échelles. De l'échelle fine à large, différents filtres et perturbations structurent les communautés du sol sur la base de différents traits. De même, aux échelles larges, les communautés se structurent en fonction des perturbations importantes (A) mais peu fréquentes (inondations, ouragan), alors que les petites perturbations fréquentes sont plus importantes (C) à une échelle fine (bioturbation). Les rétroactions entre les modèles spatiaux de l'activité biotique du sol et l'hétérogénéité des facteurs environnementaux ajoutent encore à la complexité (flèches pointillées). Adapté à partir de Ettema and Wardle (2002) et Berg (2012).

1.2.1. Structuration bottom-up : effet de la quantité et qualité de la ressource

Les communautés du sol et les réseaux d'interactions sont fortement dépendants de la quantité et de la qualité de leur ressource basale, à savoir la matière organique sénescente (litières de feuilles et racines, exsudats racinaires). Suivant l'hypothèse de productivité (Abrams 1995), les milieux offrant une plus grande quantité de ressources sont à même de supporter une plus grande abondance et diversité d'organismes (Scheu and Schaefer 1998; Chen and Wise 1999). L'abondance des oiseaux et chauve-souris dans 209 forêts européennes est par exemple mieux prédite en incluant l'abondance de leur proies potentielles (chenilles, araignées de la canopée, vers de terre) qu'en incluant uniquement des variables climatiques et de structure du peuplement forestier (Barbaro et al. 2019). En plus de la quantité, la qualité de la ressource est un paramètre important pour les communautés du sol, car elle peut notamment déterminer l'équilibre entre champignons et bactéries au sein des organismes décomposeurs. Les litières possédant un rapport C/N faible (i.e. ressource de « bonne » qualité) favorisent les bactéries, tandis qu'un rapport C/N élevé (i.e. ressource de « moindre » qualité) favorisera une dominance fongique (Lavelle and Spain 2001). Ce basculement entre

dominance bactérienne ou fongique a des conséquences importantes pour les niveaux trophiques supérieurs comme les nématodes bactérovores ou fongivores, ou encore la mésofaune qui se nourrit principalement de champignons tels que les Collembolles (Scheu 2002; Kaspari and Yanoviak 2009; Bastow 2012). Au delà du C/N, d'autres caractéristiques des litières déterminent sa qualité, telles que la teneur en lignine ou en tannins, ainsi que l'épaisseur et la dureté des feuilles après abscission. Dans des forêts du Canada, Brousseau et al. (2019) ont pu montrer que les traits de qualité de la ressource (épaisseur et dureté de la litière ou des proies) co-varient spatialement avec les traits d'acquisition de la ressource des consommateurs (largeur et puissance des mandibules des détritivores ou des prédateurs).

1.2.2. Microhabitat et microclimat

Si la quantité de litière joue un rôle important en tant que ressource, elle est également l'habitat physique d'une grande partie des organismes du sol qui vivent dans une maison faite de nourriture ("a house made of food"; Fujii et al. 2020). L'épaisseur de la couche de litière détermine ainsi l'abondance et la diversité des communautés d'invertébrés du sol (Hansen and Coleman 1998; Kaspari and Yanoviak 2009). Le nombre de microhabitat disponible dépend également de la structure tridimensionnelle de (i) la végétation herbacée pour les animaux vivant en surface du sol, des (ii) feuilles, aiguilles et bois morts pour les animaux vivant dans la couche organique, ou des (iii) pores, fissures, et galeries du sol pour les animaux vivant plutôt dans l'horizon (organo)minéral du sol (Hättenschwiler et al. 2005a; Erktan et al. 2020). Dans ces nombreux microhabitats, les organismes du sol peuvent également bénéficier de conditions microclimatiques particulières. Le microclimat se définit comme les conditions de température et d'humidité à une échelle fine (quelques décimètres) et dépend de la capacité de la canopée, de la végétation sous-arborée et du tapis forestier à tamponner les variations climatiques du milieu. Une canopée dense intercepte davantage la lumière, réduisant la quantité d'énergie et de chaleur arrivant à la strate herbacée et au sol, réduisant ainsi la biomasse et diversité de la végétation sous-arborée (Prescott and Vesterdal 2013). Ces changements de végétation ainsi qu'une plus faible température au sol peuvent substantiellement modifier les communautés de faune du sol (Henneron et al. 2015, 2017; Mueller et al. 2016). De même, une canopée plus fermée intercepte les pluies et augmente l'évapotranspiration, résultant en une diminution de l'humidité des sols (Augusto et al. 2015).

1.2.3. Les formes d'humus

L'ensemble des caractères de l'horizon du sol précédemment décrit (quantité et qualité de la litière, microclimat et microhabitats) ne sont pas indépendants (Gobat et al. 2010). Une litière de meilleure qualité chimique se décompose plus vite et s'accumule peu, limitant le nombre de microhabitats et augmentant les nutriments disponibles pour la végétation de sous-bois. Il est ainsi possible de classer les différentes configurations des horizons de surface en différents types d'humus (Ponge 2003; Zanella et al. 2011). En simplifiant, il est possible de définir trois formes d'humus (Figure 1.7) : 1) les « mull » sont caractérisés par la disparition rapide de la litière sous l'activité de la macrofaune sapro-géophage, résultant en un important mélange de l'horizon minéral et organique qui est très structuré en macro-agrégats et où vit une grande diversité d'organisme ; 2) les « moder » présentent une plus faible abondance et activité de la macrofaune, ce qui résulte en une plus grande accumulation de litière qui se structure en trois horizons : une couche de feuilles entières, une couche de feuilles fragmentées, et une couche peu épaisse et souvent discontinue de matière organique humifiée ; 3) les « mor » présentent une décomposition encore plus lente, et se caractérisent par une forte accumulation des litières à différents niveaux de transformation, se traduisant notamment par un horizon humifié continu et épais, principalement habité par des enchytréides. Ces trois types d'humus sont le résultat intégratif sur le temps long de l'action du climat, du type de roche mère, et de la végétation, sur la décomposition des déchets organiques et la formation du sol forestier. L'humus se trouve à l'interface entre l'horizon minéral et les plantes, et supporte la grande majorité des interactions plantes-animaux dans les écosystèmes forestiers, et joue un rôle clé dans le fonctionnement des écosystèmes (Facelli and Pickett 1991).



Figure 1.7 – Les différentes formes d'humus. De gauche à droite : mull, moder, et mor.

1.2.4. L'importance des arbres

L'influence de la diversité, de la composition et de la structure des communautés végétales sur les organismes du sol est de plus en plus étudiée, et les interactions plantes-animaux édaphiques sont désormais reconnues comme centrales à de nombreux processus écosystémiques (Bardgett and Wardle 2010). Bien que les premiers travaux sur le sujet aient portés sur les écosystèmes prairiaux, les effets des arbres sur la faune du sol en milieu forestier ont été le sujet de nombreuses études, les plus récentes s'intéressant à démêler les effets directs et indirects de l'identité et de la diversité des arbres sur les communautés du sol (Scheu 2005; Korboulewsky et al. 2016).

1.2.4.1. *Identité*

Un nombre important de caractéristiques des arbres est susceptible de modifier les paramètres environnementaux précédemment cités comme déterminants pour la macrofaune du sol. La phénologie de la chute de la litière, sa quantité, ainsi que sa qualité sont d'importants paramètres qui déterminent directement la qualité et la quantité de ressource ainsi que d'habitats dans le tapis forestier. Avant la sénescence, la canopée joue également important car son degré d'ouverture qui conditionne l'impact d'une espèce d'arbre sur la lumière et les précipitations qui attendront le sol et moduleront le microclimat du sol (Augusto et al. 2015). Les arbres, par la production de litière (foliaire et racinaire) et d'exsudats racinaires de différentes compositions chimiques, peuvent également influencer le pH du sol auquel sont sensibles les organismes édaphiques (Augusto et al. 2002). Par exemple, Scheu et al. (2003) ont décrit des communautés de faune du sol différentes dans des peuplements dominés par des hêtres ou des épicéas. Les auteurs ont expliqué les augmentations de biomasse de la plupart des groupes de faune par la meilleure qualité de la litière du hêtre ainsi qu'un pH plus élevé. La qualité de la litière est également déterminante pour les organismes saprophages et est déterminée par un ensemble de traits, tels que la teneur en azote, en calcium, ou encore en tannins (Swift et al. 1979; Hättenschwiler and Vitousek 2000; Berg and McClaugherty 2008).

1.2.4.2. Les types fonctionnels

Il est possible de classer les espèces d'arbre par types fonctionnels et de distinguer les arbres caducifoliés des arbres sempervirents (Monk 1966). Ces derniers produisent généralement une litière de moins bonne qualité chimique et physique, et réduisent l'humidité des sols en maintenant une canopée dense tout au long de l'année, interceptant les précipitations et augmentant l'évapotranspiration. Il est également possible de distinguer les arbres angiospermes (feuillus) des gymnospermes (conifères). Cette distinction reflète notamment l'effet d'acidification du sol des gymnospermes, ainsi que la production d'une litière de basse qualité (aiguille), qui s'accumule et constitue un épais tapis forestier (Reich et al. 2005; Augusto et al. 2015). La conversion de forêts décidues en forêts de conifères entraîne un basculement de l'écosystème d'un système productif avec une décomposition rapide de la litière vers un système conservatif où les processus/flux sont ralentis et où les stocks de matière organique et nutriments sont plus importants (Desie et al. 2019). L'importance du type fonctionnel des arbres et l'effet négatif des arbres à feuillage persistant a été démontré dans des forêts naturelles matures sur différents taxons de macrofaune (Korboulewsky et al. 2016; De Wandeler et al. 2018; Skłodowski et al. 2018; Ampoorter et al. 2019).

1.2.4.3. Le mélange d'espèce d'arbres

Etudier l'effet de la diversité spécifique des arbres sur la faune du sol est complexe. La longue durée de vie des arbres et l'espace nécessaire à leur développement rendent la réalisation d'expérimentations plus complexes et plus longues à mettre en place. Grâce à un effort international, le réseau TreeDivNet rassemble désormais 27 sites expérimentaux (1 169 540 arbres plantés sur 855 hectares) permettant la réalisation d'études *in situ* à large échelle sur l'effet de la diversité et de la composition des arbres sur le fonctionnement des écosystèmes forestiers européens (Paquette et al. 2018). Toutefois, certains de ces sites incluent un nombre limité d'espèces d'arbre ou sont encore à un stade jeune du développement de la forêt alors qu'il est connu que l'âge de la forêt influence fortement le type d'humus et les communautés du sol (Rainio and Niemela 2003; Hedde et al. 2007; Trap et al. 2011a, b). De plus, pour distinguer l'effet du nombre d'espèces d'arbres de celui de leur identité, il est nécessaire de disposer de plusieurs parcelles forestières de différents niveaux de richesse

spécifique qui varient dans leur composition pour ne pas donner trop de poids à une espèce dominante particulière (Nadrowski et al. 2010). Certains sites tel que le site FORBIO sont à cet égard un design de dilution plus que de diversité, avec une espèce toujours présente et à laquelle on associe une ou plusieurs espèces d'arbres, « diluant » son effet en diminuant sa proportion (Verheyen et al. 2013). A ce jour, les études pouvant rigoureusement tester l'effet de la diversité des arbres sur la macrofaune du sol sont donc peu nombreuses et rapportent des résultats contrastés (Scheu 2005; Oxbrough et al. 2010; Barsoum et al. 2014; Korboulewsky et al. 2016). Des études plus récentes montrent toutefois que dans des forêts naturelles matures, dont les sites étudiés dans cette thèse, la diversité des arbres est à même d'influencer l'abondance et la diversité de nombreux taxa, notamment du sol (Ampoorter et al. 2019). Les forêts mixtes peuvent effectivement supporter une plus grande abondance et diversité d'organisme édaphiques en limitant l'effet négatif de certaines espèces d'arbre. Par exemple, l'ajout d'une espèce d'arbre produisant une litière de haute qualité peut également compenser la présence d'autres espèces produisant une litière de faible qualité (Desie et al. 2020). Les peuplements mixtes offrent également une plus grande diversité de ressource et de microhabitats qu'un peuplement monospécifique (Hansen and Coleman 1998). Afin, grâce à la plasticité intraspécifique des caractéristiques de leur canopée, les arbres en mélange ont de plus tendance à croître en formant une canopée plus dense (Jucker et al. 2015) et ainsi limitent les variations microclimatiques (Mueller et al. 2016; Henneron et al. 2017).

1.3. Biodiversité et fonctionnement des écosystèmes

Comme détaillé dans les parties I et II, la faune du sol et la végétation influencent conjointement le fonctionnement du sol de leur habitat et par extension celui de l'écosystème dans lequel elles sont présentes. On peut se donc se demander ensuite comment la composition mais aussi la diversité des communautés écologiques influencent le fonctionnement de ces écosystèmes ? Après de nombreux travaux théoriques et expérimentaux, cette relation est de mieux en mieux compris mais reste d'actualité. Dès le 19^e siècle, Charles Darwin s'était intéressé à cette question :

« Si une parcelle de sol est semée avec une seule espèce d'herbe, et une parcelle similaire est semée avec des herbes de genre différent, un plus grand nombre de plante et une plus grande masse sèche d'herbe sera produite dans le second cas »

Darwin, 1859

Cette observation a pris tout son sens dans les années 1990, avec la quantification de l'érosion de la biodiversité, et un nouveau champ de recherche s'est activement intéressé à étudier le rôle de la biodiversité dans le fonctionnement des écosystèmes (BD-EF).

1.3.1. Mécanismes sous-jacents au lien entre Biodiversité et Fonctionnement des Ecosystèmes

Les premières expériences réalisées sur les liens BD-EF ont manipulé la richesse spécifique d'organismes au cycle de vie court, notamment des plantes herbacées et ont confirmé l'effet positif de la biodiversité sur la productivité primaire (Hooper et al. 2005). Les nombreuses études qui suivirent permirent d'étudier les mécanismes responsables de cette relation. Dans une communauté, les espèces diffèrent vis-à-vis de leur niche écologique, c'est-à-dire de la gamme de ressources et d'habitats qu'elles utilisent, permettant leur coexistence dans un milieu limité en ressources. Ainsi, une communauté plus diversifiée exploite les ressources d'un milieu de plus de manières différentes, et donc de façon plus complète, qu'une communauté moins diversifiée dans le même milieu. De cette « complémentarité écologique » (« complementarity effect ») peut résulter une meilleure utilisation générale des ressources et donc une plus grande productivité du système (plus grand nombre d'individus ou biomasse plus importante). Conjointement, plus une communauté est diversifiée, plus la probabilité qu'elle contienne une espèce dont l'activité favorise un processus écologique (par exemple une espèce fortement productive) augmente ; ce mécanisme est qualifié d'« effet d'échantillonnage » (« sampling effect »). Complémentarité écologique et effet d'échantillonnage sont deux mécanismes permettant d'expliquer la plus grande productivité des écosystèmes accueillant une plus grande diversité d'organismes (Loreau and Hector 2001). Les travaux portant sur les liens BD-EF montrent également que l'effet de la diversité taxonomique tend à saturer à partir d'un certain nombre d'espèce dans la communauté, du fait de l'existence d'une certaine proportion de redondance fonctionnelle entre les espèces. A l'inverse, la diversité fonctionnelle (FD), c'est-à-dire la diversité des traits des espèces, des

ressources qu'elles utilisent et des fonctions qu'elles assurent, semble être un meilleur prédicteur des processus écosystémiques (Tilman et al. 2014). Le cadre théorique du lien BD-EF a été principalement construit à partir d'expérimentations en créant parfois des communautés que l'on ne retrouve pas *in natura*. De récentes études ont toutefois montré que, même en retirant les communautés irréalistes de ces expériences, le lien positif entre biodiversité et fonctionnement des écosystèmes se maintient (Jochum et al. 2020), et se retrouve également dans les communautés naturelles (van der Plas 2019). Toutefois, les travaux portant sur le sujet sont marqués par un important biais taxonomique, avec une grande majorité des travaux ayant porté sur les plantes terrestres et les biomes tempérés, tandis que certains groupes d'organismes tels que les invertébrés du sol y ont été comparativement peu considérés (van der Plas 2019).

1.3.2. Application à la faune du sol

A ce jour, une poignée d'études s'est intéressée à l'importance de la diversité spécifique et fonctionnelle des organismes du sol pour le fonctionnement des écosystèmes. Trois d'entre elles ayant indépendamment manipulé la richesse spécifique et la dissimilarité fonctionnelle ont également trouvé un effet plus important de la diversité fonctionnelle que de la diversité taxonomique sur la minéralisation du carbone (Heemsbergen 2004; Lubbers et al. 2020) et la perte en masse des litières (Hedde et al. 2010). Ces résultats suggèrent qu'à un même niveau de richesse spécifique, les communautés constituées d'espèces plus dissimilaires (et donc plus complémentaires) minimisent le poids de la compétition interspécifique et permettent les mécanismes de facilitation qui accélèrent les processus de dégradation de la matière organique. Une étude manipulant à la fois la diversité fonctionnelle de la litière et des macroarthropodes saprophages sous différentes fréquences de précipitation a démontré un effet positif de la FD des litières et de la faune sur la perte en masse des litières, quel que soit l'humidité, appelant à davantage d'étude sur l'importance de la diversité à différents niveaux trophiques (Coulis et al. 2015a). Toutes ces études restent toutefois limitées dans leur degré de réalisme, en particulier l'étude de Lubbers et al. (2020) dont les auteurs reconnaissent que les densités de vers étaient parfois trop élevées dans certains microcosmes avec jusqu'à 1140 ind.m⁻².

1.4. Conséquences des changements globaux sur la biodiversité et le fonctionnement des écosystèmes

Les changements globaux sont multiples et regroupent les changements climatiques (augmentation des températures, de la fréquence/intensité des événements extrêmes...), les changements d'utilisation des terres, les pollutions des écosystèmes, l'érosion de la biodiversité et la multiplication des invasions biologiques. Tous ces changements n'ont pas la même ampleur, apparaissent inégalement à la surface du globe et affectent différemment le Vivant, rendant difficile l'étude de la réponse de la biodiversité soumise à ces changements. Une récente étude a manipulé conjointement 10 composantes des changements globaux et étudié la réponse du fonctionnement des communautés microbiennes du sol à un nombre croissant de facteurs cumulés. Cette étude montre que la réponse des communautés à la combinaison de plusieurs facteurs de changements globaux simultanés ne pouvait être prédite à partir des réponses à chaque facteur pris individuellement (Rillig et al. 2019). De plus, l'effet de la manipulation des conditions climatiques pour simuler de futurs changements globaux dépend du climat naturel auquel sont soumis les communautés, suggérant que prédire la réponse d'une communauté aux changements globaux nécessite de bien connaître son histoire et les perturbations auxquelles elle est soumise (Meehan et al. 2020). Ces résultats montrent les limites de nos connaissances, et l'importance de poursuivre les études sur l'effet des changements climatiques sur l'activité des organismes du sol et les processus écologiques régulés par leurs activités.

1.4.1. Changements futurs des régimes de précipitation

Le Groupe d'experts Intergouvernemental sur l'Évolution du Climat (GIEC) prévoit des changements climatiques inégaux sur la planète, notamment en terme de régime de précipitations (Stocker 2014). En Europe, il est prédit une augmentation de l'intensité, de la fréquence et de la durée des périodes de sécheresse en période estivale (Figure 1.8, Dai 2013). Plus précisément, les précipitations plus faibles dans cette région induiront une diminution importante de l'humidité des sols dans les 10cm, de l'ordre de -3 (Royaume-Uni) à -12% (bassin méditerranéen). Ces changements d'humidité du sol s'accompagnent d'une augmentation de la fréquence, de la durée et de la sévérité des événements de sécheresse

extrême sur l'ensemble de l'Europe de l'Ouest (Dai 2013). Il est urgent d'étudier la réponse des communautés végétales et animales à ces changements de régime de précipitation, ceci afin de mieux anticiper les conséquences multiples et complexes que ces changements climatiques auront sur le fonctionnement des systèmes écologiques et la production de services écosystémiques pour les populations humaines.

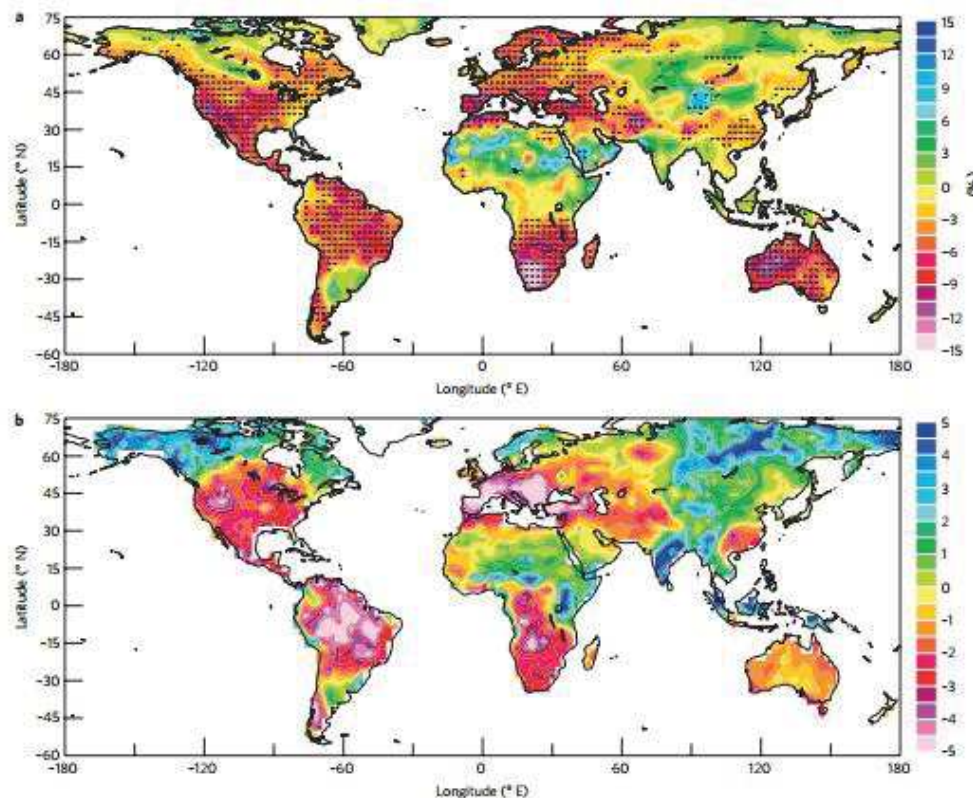


Figure 1.8 - Prédiction des changements d'humidité des sols et d'évapotranspiration. **a.** Changement d'humidité des sols dans les 10 premiers cm entre les périodes 1980-1999 et 2080-2099 sous le scénario RCP4.5 (augmentation des températures de 1.5°C). **b.** Indice moyen de sévérité de la sécheresse de Palmer (PDSI) moyenné sur 2090-2099. Une valeur de PDSI inférieure ou égale à -3.0 indique des sécheresses extrêmes par rapport au climat actuel. Extrait de Dai (2013).

1.4.2. Réponse des forêts

Les écosystèmes forestiers représentent 30% des terres émergées et sont très importants dans la régulation du climat planétaire dans la mesure où ils captent une part considérable du CO₂ atmosphérique converti en biomasse (la productivité primaire est estimée entre 8 et 30 tonnes par hectare par an), et influencent l'albédo et le cycle de l'eau (Bonan 2008). Les forêts constituent également un important réservoir de biodiversité puisqu'elles abritent la moitié des espèces animales et végétales de la planète (Shvidenko et al. 2005). Ces écosystèmes sont

toutefois très sensibles aux changements globaux car la longue durée de vie des arbres, et leur faible capacité de dispersion les rend vulnérables aux changements rapides, notamment aux modifications des régimes de précipitation, comme par exemple l'augmentation de la fréquence, de l'intensité, et de la durée des sécheresses (Lindner et al. 2010). Cependant, toutes les espèces d'arbres ne présentent pas le même degré de sensibilité aux changements climatiques, et certaines peuvent répondre de manière asynchrone, ce qui peut induire des changements de composition des forêts (Morin et al. 2008). Ces changements de composition et de diversité (principalement réduction) des forêts pourraient hautement affecter la résistance et résilience de ces forêts aux futurs changements climatiques (Scherer-Lorenzen et al. 2005).

1.4.3. Réponse des organismes du sol

La réponse des organismes du sol aux changements globaux, et notamment aux mutations climatiques, est de plus en plus étudiée, et les études sur ce sujet montrent globalement un effet négatif de la réduction des précipitations sur l'activité biologique du sol. Une méta-analyse a notamment permis de montrer une diminution de l'abondance et de la diversité des organismes du sol soumis à une réduction des précipitations, mais cet effet n'a pu être mis en évidence que dans les écosystèmes forestiers (Blankinship et al. 2011). Cela peut s'expliquer par une évapotranspiration et une interception des pluies par les arbres plus importante dans les forêts que dans d'autres types d'écosystèmes, ce qui a pour effet d'accentuer la compétition pour l'eau aussi bien pour la végétation que pour les organismes édaphiques. La réponse des organismes du sol dépend toutefois du taxon étudié et des niches et stratégies écologiques des espèces. Par exemple, si les bactéries sont fortement et négativement impactées par une diminution de l'humidité du sol, les champignons sont par contre plus résistants car les hyphes fongiques peuvent tout à fait se développer dans des milieux anhydriques (de Vries and Shade 2013). De la même façon, certains nématodes de petite taille et présentant des stratégies écologiques de type *r* (fort taux de reproduction, courte durée de vie) peuvent se montrer plus résistants que d'autres nématodes de niveaux trophiques supérieur, plus grands et de stratégie *K* (Bongers and Bongers 1998). Certains nématodes bactérivores peuvent même être actifs dans des sols au potentiel hydrique très bas, jusqu'à -1.5MPa (Yeates et al. 2002). Les macroarthropodes saprophages sont quant à eux sensibles à

la sécheresse, y compris les espèces adaptées à des milieux régulièrement soumis à des stress hydriques comme en climat méditerranéen (David and Handa 2010). Au-delà de changements de densité des populations, les macroarthropodes saprophages montrent une diminution d'activité à des taux d'humidité de l'air ambiant plus bas (Dias et al. 2012), bien qu'ils semblent être plus sensibles à des changement de fréquence que de quantité de précipitations (Joly et al. 2019). Une récente étude où deux espèces saprophages communes, *Armadillidium vulgare* et *Glomeris marginata*, ont été installées seules ou en mélange dans des microcosmes et soumis à différentes fréquences et quantités de précipitations dans une forêt mixte écossaise a montré qu'en conditions stressantes, l'interaction synergistique positive entre les deux espèces disparaît, voire devient négative (Joly et al. submitted). Les conditions climatiques peuvent donc altérer l'activité des espèces et donc leur rôle dans les processus écosystémique, ainsi que les interactions entre espèces mais nos connaissances sur ce sujet restent limitées. Davantage d'études sont nécessaires pour mieux comprendre le lien entre diversité de la faune du sol et fonctionnement des écosystèmes dans différents contextes climatiques.

1.5. Questions de recherche et objectifs

Cette thèse a pour objectif de contribuer à la compréhension des interactions biotiques entre les plantes et la faune du sol dans des forêts aux contextes pédoclimatiques contrastés et sous l'influence de stress environnementaux tels que l'allongement des périodes de sécheresse. Une première approche comparative vise à décrire les facteurs de contrôle des communautés de macrofaune du sol dans des forêts européennes, en mettant l'accent sur l'importance de la diversité spécifique des arbres et de leur type fonctionnel (chapitres 1 et 2). Dans un second temps, des expérimentations en conditions contrôlées ont considéré les interactions trophiques entre les litières d'arbres et la faune saprophage, et leurs conséquences pour la transformation de la matière organique (chapitre 3), puis d'étudier les interactions entre macrofaune et nématodes du sol dans un contexte de changement climatique (chapitre 4). Cette thèse s'appuie à la fois sur des données collectées au champ et sur des résultats d'expérimentations en conditions contrôlées.

Question 1 : Quelle est l'importance relative de la diversité et du type fonctionnel des arbres et des conditions microenvironnementales sur la composition et la structure des communautés de macrofaune du sol dans les forêts européennes ?

Hypothèse 1.1 : l'abondance et la diversité de la macrofaune sont plus élevées en forêts mixtes que pures. Cette hypothèse s'appuie sur l'idée que les mélanges d'espèces augmentent la probabilité d'inclure une espèce d'arbre aux traits favorables pour la macrofaune, et fourni par ailleurs une diversité plus importante de microhabitats et de ressources trophiques.

Hypothèse 1.2 : les communautés de macrofaune sont largement structurées par les conditions microclimatiques et la disponibilité des microhabitats, qui sont à leur déterminées par le type fonctionnel dominant des arbres (décidus vs persistant). On s'attend en effet à observer une augmentation de l'abondance et diversité des invertébrés édaphiques sous les arbres permettant une plus grande ouverture de la canopée et l'établissement d'une strate herbacée fournissant des microhabitats et des ressources diversifiés.

Hypothèse 1.3 : la réponse de la macrofaune dépend de son niveau trophique. On s'attend en effet à ce que les organismes saprophages soient plus sensibles que les prédateurs aux changements de composition en arbres, car sont directement reliés aux arbres par interactions trophiques, alors que les prédateurs dépendent seulement des microhabitats et du microclimat maintenu par les arbres.

Après cette approche globale sur l'ensemble de la macrofaune du sol, le second chapitre se concentre sur l'influence de la diversité végétale sur la structure fonctionnelle des communautés de coléoptères Carabidae.

Question 2 : comment se structure fonctionnellement les communautés de coléoptères Carabidae dans des forêts de différentes composition en arbres et aux conditions stationnelles différentes ?

Hypothèse 2.1 : les parcelles de forêts mixtes fourniront davantage de microhabitats plus diversifiés et une qualité de litière en moyenne meilleure pour les proies des carabiques favorisant une plus grande proportion de généralistes d'habitat et régime alimentaire, et une plus grande diversité fonctionnelle.

Hypothèse 2.2 : la proportion d'arbres à feuillage persistant diminue la qualité du sol et de la litière, et la diversité de la végétation sous-arborée, réduisant la diversité fonctionnelle des carabiques pour favoriser les espèces spécialistes des forêts et zoophages. La diminution associée de fertilité du milieu induira une diminution de la taille moyenne des carabiques.

Hypothèse 2.3 : la fermeture de la canopée filtre pour les espèces spécialistes des forêts, incapable de voler (aptères ou brachyptères) et meilleures marcheuses (plus grande longueur de jambe par rapport à la longueur totale).

Hypothèse 2.4 : la qualité du sol, reliée à la productivité de la parcelle va positivement influencer la masse corporelle moyenne.

Hypothèse 2.5 : la biomasse et diversité de végétation sous arborée ainsi que la biomasse de proie potentielle à la surface du sol vont respectivement favoriser les espèces généraliste en favorisant les espèces graminivore, et les espèces zoophages.

Suite à cette approche comparative sur les traits des coléoptères carabiques, deux approches expérimentales sont utilisées pour s'intéresser aux traits et au rôle des macroinvertébrés sapro-géophages et leurs interactions biotiques.

Question 3 : est ce que les préférences alimentaires des macroarthropodes saprophages sont prédictibles à partir des propriétés physico-chimiques des feuilles de litière, et ces préférences ont-t-elles des conséquences pour les propriétés de leurs déjections ?

Hypothèse 3.1 : les macroarthropodes saprophages préfèrent les litières riches en nutriments, de faible teneur en tannins, à forte capacité de rétention d'eau et faible épaisseur.

Hypothèse 3.2 : les propriétés des boulettes fécales dépendent de la composition du régime alimentaire des macroarthropodes, de leurs besoins nutritionnels et de leur capacité à digérer certains constituants complexes de la litière comme les tannins

Hypothèse 3.3 : chaque espèce de macroarthropodes saprophages induira une transformation de la matière organique différente du fait de traits physiologiques différents d'une espèce à l'autre.

Le dernier chapitre de la thèse abordera l'étude des interactions macro-microfaune et plus précisément l'effet de la diversité de la macrofaune sapro-géophage sur les communautés de nématodes soumis à une sécheresse prolongée..

Question 4 : est-ce qu'une plus grande diversité fonctionnelle de la macrofaune sapro-géophage limite les effets de la sécheresse prolongée sur les nématodes ?

Hypothèse 4.1 : une sécheresse prolongée diminue l'abondance des nématodes, notamment aux plus hauts niveaux trophiques (prédateurs et omnivores), favorisant les nématodes microbivores plus résistants aux stress environnementaux.

Hypothèse 4.2 : une macrofaune plus diversifiée fonctionnellement favorise l'abondance et la diversité des nématodes, notamment bactérivores et limite l'impact négatif de la sécheresse

Hypothèse 4.3 : tous les groupes de macrofaune n'induiront pas la même réponse des nématodes avec un effet plus grand des ingénieurs de l'écosystème (vers de terre anéciques et endogés) qui affectent le sol de façon plus importante et variée que les transformateurs de litière (isopodes et diplopodes).

1.6. Le projet SoilForEUROPE

Ma thèse s'inscrit dans le projet SoilForEUROPE « Prédire la biodiversité du sol des forêts européennes et son fonctionnement face aux changements climatiques actuels » (coordination Stephan Hättenschwiler – CEFE Montpellier) financé dans le cadre de l'appel à proposition européen BiodivERsA 2015. Ce projet a pour premier objectif de caractériser la diversité des communautés de macrofaune, mésofaune, microfaune et microorganismes dans 64 forêts de différentes compositions spécifique d'arbre sur quatre sites distribués le long d'un gradient latitudinal (Figure 1.9-10). Dans un second temps, plusieurs approches expérimentales (interception de pluie ou arrosage dans des forêts artificielles plantée, et dans cette thèse : mésocosmes et microcosmes en enceintes climatiques, Figure 1.11-12) sont employées afin de déterminer l'activité des organismes du sol en fonctions de différents stress hydriques, et mesurer dans quelle mesure la diversité des arbres ou de la faune du sol permet un meilleur maintien des processus écosystémiques face à ces perturbations. Ce projet fait suite au projet FunDivEUROPE qui a déjà décrit de manière extensive 209 placettes forestières sur 6 pays (dont celles du projet SoilForEUROPE) pour étudier l'effet de la diversité spécifique

et fonctionnelle des arbres sur de multiple fonction de l'écosystème et les communautés de multiples taxons (plantes herbacées, invertébrés, mammifères, oiseaux, chiroptères...). Les modalités de sélection et les caractéristiques des placettes ainsi que des dispositifs expérimentaux sont décrits plus précisément pour chaque chapitre et dans Baeten et al. (2013).

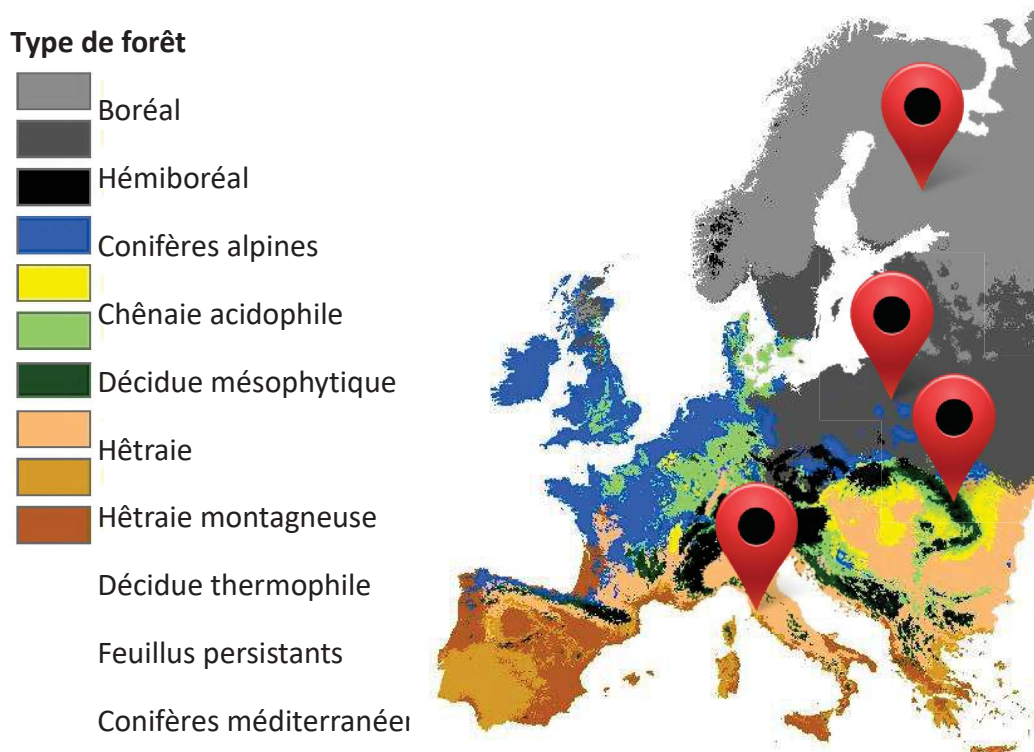


Figure 1.9 – Carte de la distribution géographique des quatre sites échantillonnés dans l'étude. Du nord au sud : forêts boréales de Karelle du nord (Finlande), forêts hémiboréales composées de feuillus et conifères en mélange de Bialowieza (Pologne), forêts montagneuses en mélange d'hêtre de Râșca (Pologne), et les forêts thermophiles méditerranéennes de la Colline Metallifère (Italie). Carte issue de Casalegno et al. (2011).

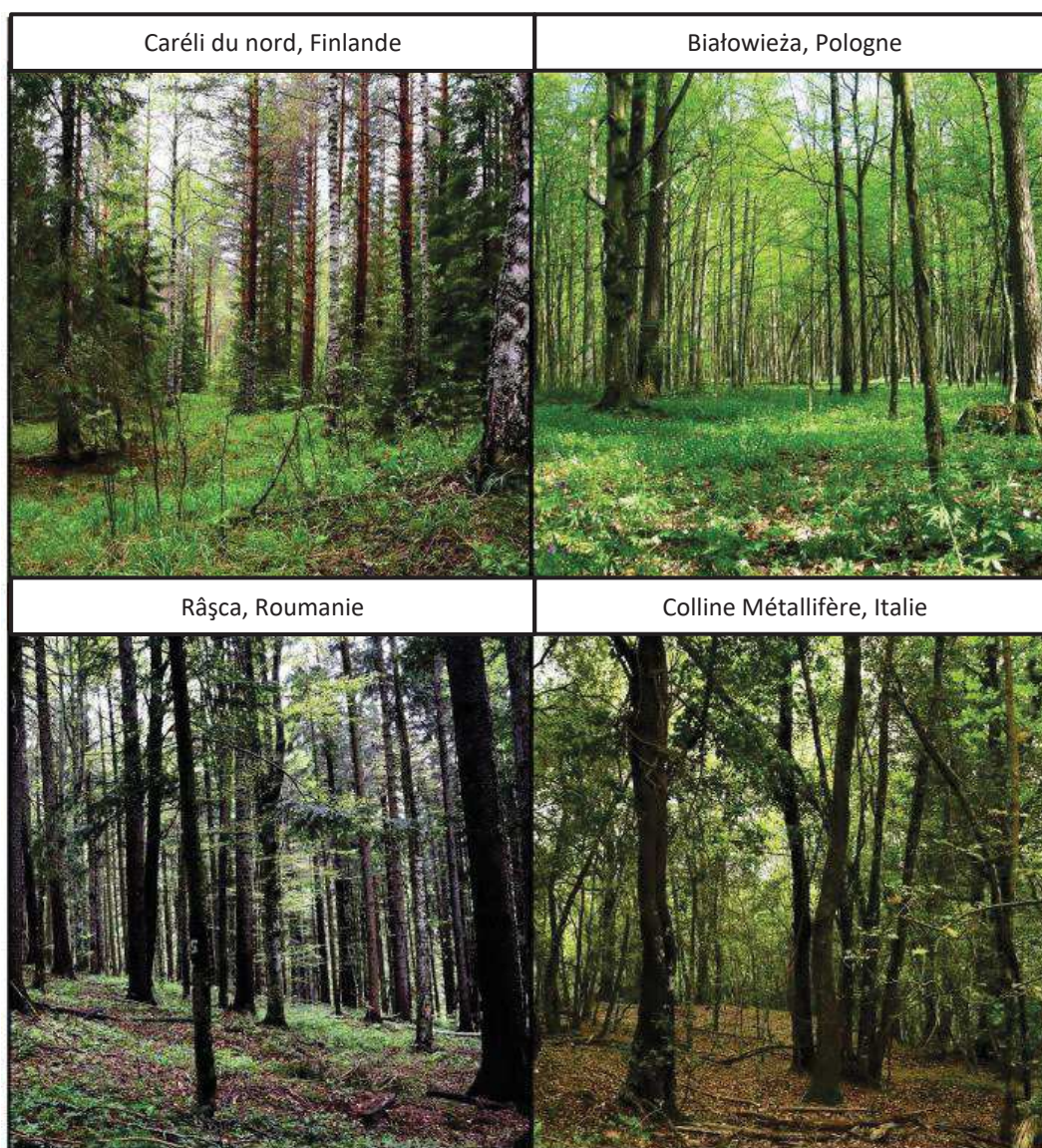


Figure 1.10 – Photographies des principaux types de forêts échantillonnées dans l'étude. Crédit photo : Lauren Gillespie.



Figure 1.11 – Photographies des enceintes climatiques et des microcosmes (ici *Armadillo officinalis*) pour les arthropodes pour la première expérimentation



Figure 1.13 – Plateforme expérimentale des mésocosmes à l’Ecotron européen de Montpellier. En haut : ensemble des mésocosmes alignées en deux rangées orientées Est-Ouest. En bas à gauche : un mésocosme avec une ombrière blanche pour simuler la réduction de lumière par la canopée des arbres matures. En bas à droite : vu des jeunes arbres le 10 octobre 2020 au moment de la sénescence des feuilles de l’érable de Montpellier.

Chapter 1

Relative importance of tree diversity, tree functional type, and microenvironment for soil macrofauna communities in European forests

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Abstract

Tree and soil fauna communities are major drivers of many forest ecosystem processes. Tree species diversity and composition also shape soil fauna communities, but their relationships are poorly understood, notably whether or not soil fauna diversity depends on tree species diversity. Here, we characterized soil macrofauna communities from forests composed of either one or three tree species, located in four different climate zones and growing on different soil types. Using multivariate analysis and model averaging we investigated the relative importance of tree species richness, tree functional type (deciduous vs. evergreen), litter quality, microhabitat and microclimatic characteristics as drivers of soil macrofauna community composition and structure. We found that macrofauna communities in mixed forest stands were represented by a higher number of broad taxonomic groups that were more diverse and more evenly represented. We also observed a switch from earthworm-dominated to predator-dominated communities with increasing evergreen proportion in forest stands, which we interpreted as a result of a lower litter quality and a higher forest floor mass. Finally, canopy openness was positively related to detritivore abundance and biomass, leading to higher predator species richness and diversity probably through trophic cascade effects. Interestingly, considering different levels of taxonomic resolution in the analyses highlighted different facets of macrofauna response to tree species richness, likely a result of both different ecological niche range and methodological constraints. Overall, our study supports the positive effects of tree species richness on macrofauna diversity and abundance through multiple changes in resource quality and availability, microhabitat, and microclimate modifications.

Keywords

Community ecology, forest ecosystems, biodiversity-ecosystem functioning, aboveground-belowground linkages

2.1. Introduction

Research on the interactions between biodiversity and ecosystem functioning seeks to understand the links between community diversity and ecosystem processes, across terrestrial and aquatic ecosystems (Gessner et al. 2010; van der Plas 2019). The study of forest ecosystems dominated by tree as long-lived organisms is challenging in this context, in particular when using experimental approaches. Yet, it is of considerable importance given that these ecosystems support a multitude of key ecosystem services, such as timber production, watershed protection and carbon sequestration (Scherer-Lorenzen et al. 2005). These services depend strongly on forest stand tree species richness, as well as on tree taxonomic and functional type (e.g. evergreen vs. deciduous; Gamfeldt et al. 2013). In addition, tree diversity may determine the abundance and diversity of other groups of organisms (Ampoorter et al. 2020) that could affect ecosystem processes. Especially, trees shape communities of soil invertebrates, which are key regulators of soil functioning and primary productivity (Wardle 2004; Wall et al. 2012). However, the direct and indirect mechanisms underlying soil invertebrate responses to tree species diversity and composition remain poorly understood, even in temperate forest ecosystems (Korboulewsky et al. 2016).

Trees can influence soil fauna through the provision of energy and matter via living and dead plant products such as leaf and root litter, dead wood, and rhizodeposition. Many soil organisms such as macrodetritivores (earthworms, millipedes, woodlice) feed directly on plant debris (Lavelle and Spain 2001), imposing stoichiometric constraints with lower and narrower carbon to nutrient ratios in animal biomass than that of their feeding resource (Sterner and Elser 2002). Resource nutrient concentrations are therefore particularly important as they determine litter palatability for macrodetritivores, and have important consequences on the structure of their communities (Ott et al. 2014). In mixed forest stands, litter may be of overall higher quality relative to monospecific stands when tree species with high quality litter may compensate for those with low nutrient concentrations or high contents in recalcitrant compounds such as polyphenols or lignin. Hence, in the litter layer of mixed forests stands, the higher resource diversity and the complementary resource use of litter of different quality by macrodetritivores may better enable covering animal stoichiometric demands (Handa et al. 2014). Another pattern often highlighted in the literature is the negative effect of evergreen

trees on soil fauna communities (Reich et al. 2005), which can be related to the low litter quality of most evergreen species. Additionally, other evergreen traits such as leaf life span and the phenology of leaf senescence together determine tree canopy properties which affect microhabitats and microclimate conditions at soil surface (Monk 1966).

Beyond litter quality and its consequences for the heterotrophic soil food web, different tree species also vary in a number of physical characteristics that may influence soil fauna communities. For instance, differences in leaf size, leaf shape, and amount of litterfall (including deadwood), determine the total volume of habitats, and their spatial organization for both detritivore and predator species (Aubert et al. 2006, Kaspari and Yanoviak 2009). The structural complexity of litter layers, and the resulting diversity of microhabitats for the soil fauna, also vary from one tree species to another and are likely higher in mixed than pure stands (Hättenschwiler et al. 2005b). This may contribute to an increase in abundance and diversity of soil invertebrates in mixed when compared to monospecific forest stands (Hansen and Coleman 1998), especially when the mixed stands include deciduous broadleaved trees among evergreen conifers (Kaneko and Salamanca 1999). The influence of the previously mentioned litter properties (nutrient content, shape, litter layer depth) on soil and forest floor properties and on invertebrate communities also varies with tree canopy diversity and composition (Augusto et al. 2002; Ponge 2003).

Tree canopy openness is also an important but overlooked forest stand characteristic that has important effects on forest floor conditions. By modulating light availability at the soil surface, canopy openness may influence soil communities by altering forest floor microclimate and understory vegetation (Prescott and Vesterdal 2013; Henneron et al. 2015; Mueller et al. 2016). This again can differ depending on tree species diversity that can affect canopy openness and litter production through increased canopy packing, as was reported for different European forests (Jucker et al. 2015). In addition, evergreen tree species distinctively affect microclimatic conditions, in particular through a permanent canopy cover, and high leaf area index (LAI) all year round which leads to higher rainfall interception and evaporation and thus drier soils (Augusto et al. 2015).

Characterizing soil fauna responses to the diversity and composition of the standing vegetation is thus complex and often made even more difficult by taxonomic impediments

and our lack of knowledge of certain taxa. Indeed, it is difficult if not impossible to obtain rapid and reliable taxonomic assignments at a species level for most of the soil biota (Decaëns 2010). A classic strategy to avoid this problem in soil macrofauna studies is to target assignments to higher taxonomic ranks, which allows the whole community to be considered without prior selection of target taxa (Williams and Gaston 1994, Andersen 1995). Another option is to make species-level identifications possible by restricting the study to a small number of taxa, for which taxonomic expertise is available, that are further assumed to be representative of the whole community or of a particular trophic group thereof. The implication of each of these approaches for our ability to describe community patterns reliably, and the importance of the level of taxonomic resolution they imply, has never been formally addressed with regard to soil fauna. However, it is probable that some of these patterns (e.g. diversity – area, or diversity - available energy relationships) may vary in their shape depending on the fundamental taxonomic units of the study, which could consequently affect observed community responses to environmental gradients (Williams and Gaston 1994; Kaspari 2001; Storch and Šizling 2008).

In this study, we described soil macrofauna communities in forest plots composed of either a single dominant tree species or three co-dominant tree species in four different pedoclimatic zones ranging from boreal to Mediterranean. These plots were part of an existing network of natural forest plots with different tree species richness and composition across Europe (Baeten et al. 2013). We hypothesized that (H1) soil macrofauna abundance and diversity is higher in mixed species than in single species forests, likely by increasing the probability of including a tree species providing a high quality litter. We further hypothesized that (H2) soil communities are structured by litter traits as well as microhabitat and microclimatic conditions. We thus expected to find higher macrofauna diversity and abundance with increasing litter quality, canopy openness and soil quality. Forest floor thickness is expected to positively and negatively influence predator and detritivore abundance, respectively. Because of the tighter trophic link between litter layer characteristics and detritivore communities than predator communities (Scherber et al. 2010), we expected (H3) stronger responses to tree species diversity and composition in detritivore than predator communities. We finally hypothesized that (H4) describing soil fauna communities using different levels of

taxonomic resolution will highlight different facets of their responses to tree stand properties and microenvironmental variables.

2.2. Material and methods

2.2.1. Study sites and tree stand composition

The study was carried out within the framework of the SoilForEUROPE project in four forest sites selected to represent four major European forest types along a broad climatic gradient in Europe: thermophilous deciduous forests (Colline Metallifere, Italy), mountainous deciduous forests (Râșca, Romania), temperate mixed coniferous and broadleaf forests (Białowieża, Poland), and boreal forests (North Karelia, Finland). The sampled plots are part of the FunDivEUROPE exploratory platform (Baeten et al. 2013) excluding within site variation in climate, soil and land use history between plots and specifically designed to disentangle the species diversity and identity effect in the biodiversity - ecosystem functioning relationship (Nadrowski et al. 2010). In each site, replicated forest plots of 30x30m were selected to represent either monospecific stands (34 plots) or three species mixtures (30 plots), further referred to as pure and mixed stands, respectively. Selected tree species (*i.e.* target species) are 13 locally dominant and representative tree species, including evergreen conifers and evergreen or deciduous broadleaved trees (Table 2.1). These plots were selected in 2012 during the FunDivEUROPE project and relative basal area of tree species was re-estimated in 2018 for this study. The relative proportion of tree species was based on their relative basal area, and non-targeted species basal area in the plot was kept below 5%. In each plot we selected three subplot based on tree triplets forming a triangle of three individual trees with a minimal diameter at breast height of 5cm, composed of either the same target species in the pure stands or the three target tree species in the mixed stands (Fig. S2.1).

Table 1 – Description of the four sample sites, including the tree species pool, and site-specific sampling design. Soil measurements are from the first 10 cm of mineral soil

	Finland	Poland	Romania	Italy
Site description				
Latitude, longitude (°)	62.9, 29.9	52.8, 23.9	47.3, 26.0	43.2, 11.2
Area ^a (km ²)	1447	346	4.26	216
Altitude (m)	139.4±36.6	165.7±12.6	891.8±96.4	405.8±60.5
Date of sampling	2017/06/12-16	2017/05/05-10	2017/05/22-28	2017/04/10-16
MAT ^b (°C)	2.0±0.3	6.9±0.1	5.5±0.5	13.4±0.3
MAP ^b (mm)	632±6	597±4	692±25	738±43
Soil type	Podzol	Cambisol/Luvisol	Eutric Cambisol	Cambisol
Sand (%) ^I	48.2±6.2	65.5±7.5	12.9±9.4	17.2±6.4
Silt (%) ^I	46.6±5.6	28.7±6.3	59.6±4.9	64.7±4.9
Clay (%) ^I	5.1±0.8	5.8±1.6	27.4±6.1	18.1±5.4
C (mg.g ⁻¹ dry soil)	37.8±11.5	28.4±5.3	49.2±16	50.4±13.4
N (mg.g ⁻¹ dry soil)	1.7±0.6	1.7±0.2	3.5±1	2.6±0.9
pH	3.9±0.3	3.8±0.3	4.6±0.7	4.6±1.1
Bulk density (g.cm ⁻³)	1.03±0.09	1.02±0.07	0.93±0.06	0.88±0.07
Number of mono-specific plots	6	6	8	10
Number of mixed plots	3	14	8	9
Tree species pool				
(1) <i>Abies alba</i>			x	
(1) <i>Picea abies</i>	x	x	x	
(1) <i>Pinus sylvestris</i>	x	x		
(2) <i>Quercus ilex</i>				x
(3) <i>Acer pseudoplatanus</i>			x	
(3) <i>Betula pendula/pubescens</i>	x	x		
(3) <i>Carpinus betulus</i>		x		
(3) <i>Castanea sativa</i>				x
(3) <i>Fagus sylvatica</i>			x	
(3) <i>Ostrya carpinifolia</i>				x
(3) <i>Quercus petraea</i>				x
(3) <i>Quercus robur</i>		x		
(3) <i>Quercus cerris</i>				x

^a Area was obtained from the polygon area joining most distant plots within each country, using Google Earth

^b MAT: mean annual temperature, MAP: mean annual precipitation, from WorldClim. ^I data from SoilForEUROPE project; ^{||} data from FunDivEUROPE project. (1) Evergreen needle-leaf, (2) evergreen broadleaf, (3) deciduous broadleaf

2.2.2. Invertebrates sampling and community descriptors

Sampling was conducted in 2017 during the phenological spring at each of the four sites. In each plot, soil macrofauna was sampled by excavating one soil block of 25x25x10cm within each tree triplet (i.e. three soil blocks per plot). Invertebrates were hand sorted in the field, and immediately fixed and preserved in 70% ethanol. They were further assigned to broad taxonomic groups (usually orders), with additional consideration of trophic position or ecological categories when relevant. This resulted in 16 groups: Araneae, predatory Coleoptera (Carabidae adults and larvae, Staphylinidae), Opilionidae, Dermaptera, Chilopoda, Blattodea, rhizophagous Coleoptera (larvae of Melolonthinae, Curculionidae, Elateridae), coprophagous Coleoptera (Geotrupinae), endogeic, epigeic, and anecic Lumbricidae, Diplopoda, Isopoda, Diptera larvae, Gastropoda, and Lepidoptera larvae. Species level identifications were done for all Lumbricidae, Isopoda, Diplopoda, Chilopoda, and Araneae specimens. For the few individuals for which this was not possible, genus or family levels were kept for the analysis; as this only concerned a small fraction of specimens, these higher rank taxonomic identifications were treated without distinguishing them from species-level identifications. All invertebrates were counted per broad group or species and weighed individually to the nearest 0.01mg after gently drying them with a paper towel. The abundance and biomass of the 16 different groups is given in Table S2.1. We then organized the data into three different matrices: one with the numbers of individuals per plot for each broad group, further referred to as “*all macrofauna*”, and two with the numbers of individuals per plot and per species (or finest level achieved) for the detritivore and predator groups previously mentioned, further referred to as “*detritivore assemblage*” and “*predator assemblage*”, respectively (taxa list in Table S2.2).

From these three matrices, we calculated several community descriptors: taxonomic richness (S) Pielou’s evenness (J; Pielou 1966), and Hill_{q=1}’ diversity (D₁). D₁ was obtained with the formula:

$$D_q = \left(\sum_{i=1}^S p_i^q \right)^{\frac{1}{1-q}} \quad (1)$$

where S is the total number of taxa (i.e. fundamental taxonomic units: broad groups or species depending on the matrix), *p* the proportion of taxa *i* and *q* the “order” of the diversity. The order *q* determines the diversity index sensitivity to common and rare taxa with values of *q*

below or above one giving diversities highly sensitive to rare or common taxa, respectively (Jost 2006). We choose $q=1$ and even though Eq. 1 is not defined when the diversity order is one its limit exists and equals:

$$D_1 = \exp\left(-\sum_{i=1}^S p_i \ln p_i\right) = \exp(H) \quad (2)$$

This is the exponential of Shannon entropy which has the advantage of being relatively insensitive to rare or common taxa. All analyses were done using R software v.3.5.2 (R Core Team 2019) with the individual forest plots as replication units (i.e. the three samples per plot were pooled for calculations). Community descriptors were calculated with the *diversity* function of the *vegan* package (Oksanen et al. 2019).

2.2.3. Selection of predictor variables

The predictor variables used in this study are summarized in Table S3, and protocols of variable acquisition are detailed in Appendix 1. Tree richness was included in the analyses as a factor (one or three tree species), and we assessed the effect of tree functional type by using the relative basal area of evergreen species across the three tree triplets. Other predictor variables (i.e. leaf litter traits, microenvironmental characteristics, and soil properties) were summarized by computing three Principal Components Analysis (PCA) ordinations (Fig. S2.2) with the *prcomp* function from the package *factoextra* (Kassambara 2019). The scores of the forest plots on the retained axes of each PCA were then used as synthetic environmental variables to further explain the structure and composition of macrofauna communities. Pearson correlation between all predictor variable is given in Figure S2.3.

Litter traits included the concentrations of cellulose, lignin, polyphenols, nitrogen, and calcium measured in freshly fallen leaf litter of all tree species for each country independently (i.e. we used country mean trait value for each tree species). PCA was computed with community weighted means of these traits (Garnier et al. 2004a), using tree basal area over the three triplets as a measure of the relative proportion of each species. We kept the first PCA axis which accounted for 49.5% of overall variance and represented a “*litter quality*” gradient from low-quality associated with high concentrations of lignin and cellulose (negative scores) to high-quality associated with high nitrogen and polyphenol concentrations (positive scores) (Fig. S2.2A).

The microenvironmental variables included forest floor mass, biomass of understory vegetation and volume of coarse deadwood debris per unit ground area, and the leaf area index of canopy trees as a proxy of canopy closure. Here, to include enough variance in microhabitat and microclimate properties, we kept the first two PCA axes, explaining 38.2% and 26% of the overall variance, respectively. The first axis corresponded to a switch from plots with a high understory vegetation biomass (negative scores), to plots with most of the soil covered by a thick forest floor (positive scores), and is for simplicity further referred to as “*forest floor mass*”. The second axis reflected “*canopy openness*”, with closed canopy plots having negative scores on this axis (Fig. S2.2B).

Soil characteristics in the top 10cm of mineral horizon included bulk density, pH (determined in a CaCl_2 solution), clay content, carbon content, and C/N ratio. We kept the first axis which explained 52.5% of the overall variance and represented a gradient of “*soil quality*”, with sites having negative scores being characterized by more compact, acidic and C-poor soils (Fig. S2.2C).

2.2.4. Statistical analysis

To test the effect of tree stand properties and environmental variables on the whole macrofauna, detritivore, and predator community composition, we calculated the Bray-Curtis dissimilarity matrix of the three matrices and performed a partial distance-based Redundancy Analysis (dbRDA; Legendre and Anderson 1999) with *capscale* function of the *vegan* package, and including the country as a random factor with the argument *condition* (Borcard et al. 2018). The significance of the predictor variable and of the ordination along each axis was assessed using permutation tests (*anova* function of the *stats* package, R Core Team), constraining the permutation within countries (4999 permutations, *how* function in *permute* package; Besag and Clifford 1989).

To separately test the effects of (H1) tree stand properties and (H2) microenvironmental variables, we modeled the response of each community descriptor using a MultiModel Inference (MMI) approach (Burnham et al. 2002) by consecutively building a reduced model (M1) with only tree species richness and functional type and a complete model (M2) with also microenvironment variable:

$$Y \sim \text{Tree SR} + \text{Evergreen \%} + 1 | \text{Country} \quad (\text{M1})$$

$$Y \sim \text{Tree SR} + \text{Evergreen \%}$$

$$+ \text{Litter quality} + \text{FF mass} + \text{Canopy openness} + \text{Soil quality} + 1 | \text{Country}$$

$$(\text{M2})$$

where Y is one of the 15 response variables (i.e. taxonomic richness, Hill_{q=1} diversity, evenness, abundance, and biomass calculated separately for the whole macrofauna and detritivore and predator assemblages). The list of terms preceded by the “~” are the explanatory variables (with Tree SR= tree species richness; Evergreen %= percentage of evergreen basal area; Litter quality= PC1 of litter traits; FF mass= PC1 of microenvironmental variables; Canopy openness = PC2 of microenvironmental variables; Soil quality= PC1 of soil properties; PC refereeing to the plot score on the axes of PCA of environmental variables as defined in the previous section), and “1|Country” refers to the belonging to countries included as random factor. We used Generalized Linear Mixed Models with the *glmmTMB* function of the *glmmTMB* package (Magnusson et al. 2019) and checked for residual normality and homoscedasticity. Abundance data were log(1+x) transformed since modeling residuals distributions (Poisson or negative binomial family) did not meet model assumptions (Ives 2015). In both model steps (M1 and M2), best models were selected based on the Akaike Information Criterion for small sample size (AICc, *dredge* function in the *MuMIN* package), keeping all models within $\Delta\text{AICc} < 6$ (Harrison et al. 2018a). Predictor estimates were obtained by averaging their value across the models in which the predictor appeared to avoid estimate value shrinkage towards zero (Harrison et al. 2018a). Estimates were standardized (β_{st} scale-standardization) to allow cross model comparisons of predictor effects. To quantify to what extent including microenvironmental variables improve community descriptors modeling, we compared the best model obtained from the reduced (M1) and complete (M2) model. These two best models were compared on the basis of the additional variance explained by including indirect effects by quantifying explained variance by fixed effects (R^2_{m}) and by fixed and random effects (R^2_{c} ; Nakagawa and Schielzeth 2013), and AICc.

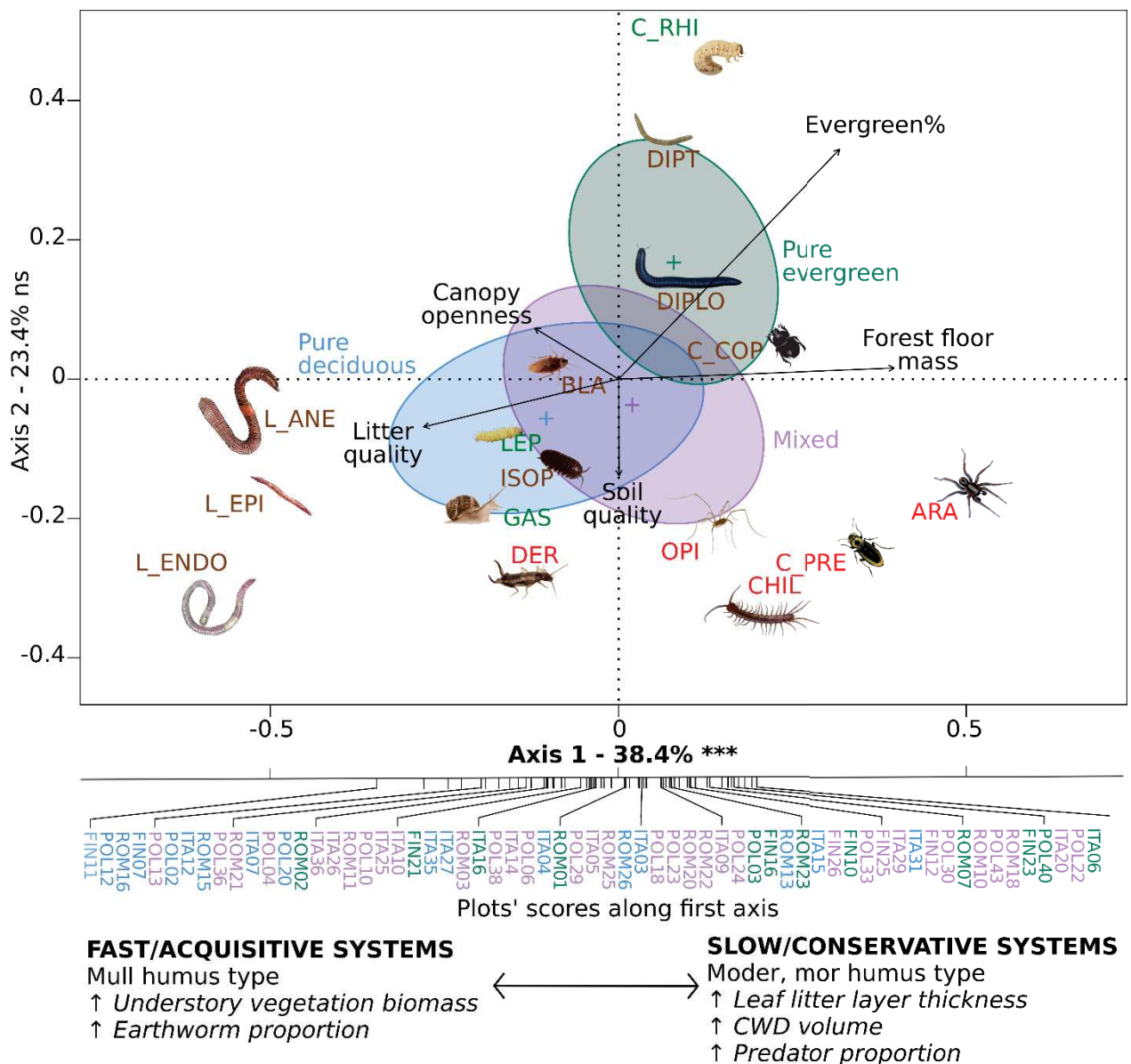


Figure 2.1 – dbRDA biplot of the whole macrofauna community. Abbreviations: ARA= Araneae, C_PRE= Coleoptera Predaceous, C_RHI= Coleoptera Rhizophagous, GAS= Gasteropoda, CHIL= Chilopoda, L= Lumbricidae, EPI= Epigeic, ANE= Anecic, ENDO= Endogeic, DIPLO= Diplopoda, ISOP= Isopoda, OPI= Opilionidae, DER= Dermaptera, BLA= Blattaria LEP= Lepidoptera Larvae, DIPT= Diptera Larvae, CWD= coarse deadwood debris. Name colors represent predaceous (red), saprophagous (brown), and herbivorous (light green) groups. Solid black arrows represent significant predictor variables after permutational ANOVA. Explained variance (%) and level of significance of each axis is shown in the axis title. Ellipses correspond to forest systems levels: pure deciduous (light blue), mixed (purple), and pure evergreen (dark green) stands. Plot' scores along first axis are represented below and color correspond to forests systems following the same codes as the ellipses. Illustration credit www.lesbullesdemo.fr.

2.3. Results

We collected a total of 2951 soil invertebrates belonging to 16 broad groups, with an average of 237.6 ± 98.9 individuals per square meter in Finland, 246.1 ± 106 in Poland, 300 ± 111.8 in Romania, and 204.1 ± 76.4 in Italy. Among the identified specimens, roughly one sixth of all individuals collected (504 individuals) were detritivores assigned to 14 species of Lumbricidae, 10 of Isopoda, and 20 of Diplopoda, and a bit more than one fourth (803 individuals) were predators assigned to 90 species of Araneae and 49 of Chilopoda.

2.3.1. Community composition

At a coarse level of taxonomic resolution, whole macrofauna communities were organized along the first axis of the dbRDA (Fig. 2.1), which explained 38.4% of overall variance ($p < 0.001$, Table S2.4) and was mainly driven by litter quality, evergreen proportion, and forest floor mass. Plots with negative scores on the first axis were characterized by high understory biomass, thin forest floor layer, high litter chemical quality, and low evergreen proportion, and they supported high abundance of earthworms of all three ecological types (i.e. endogeic, epigeic, and anecic). Plots with positive scores were dominated by evergreen tree species, presented a thick forest floor layer, a high amount of coarse deadwood debris, and harbored a relatively high abundance of predators (Araneae, Chilopoda, predatory Coleoptera, Opiliones). The second axis explained 23.4% of overall variance ($p = 0.075$) and highlighted the effect of soil quality on macrofauna communities. Plots with positive scores were characterized by low clay and carbon content, lower pH associated with evergreen tree dominance, and harbored comparatively higher densities of rhizophagous Coleoptera, Diptera larvae, and Diplopoda. The same analysis on detritivore and predator assemblages did not reveal any significant ordination (dbRDA_{Detritivore} axis 1 $p = 0.13$, dbRDA_{Predator} Axis 1 $p = 0.06$, Fig. S4, Table S2.4), meaning that the predictors considered in our study did not significantly explain community composition at the finer level of taxonomic resolution.

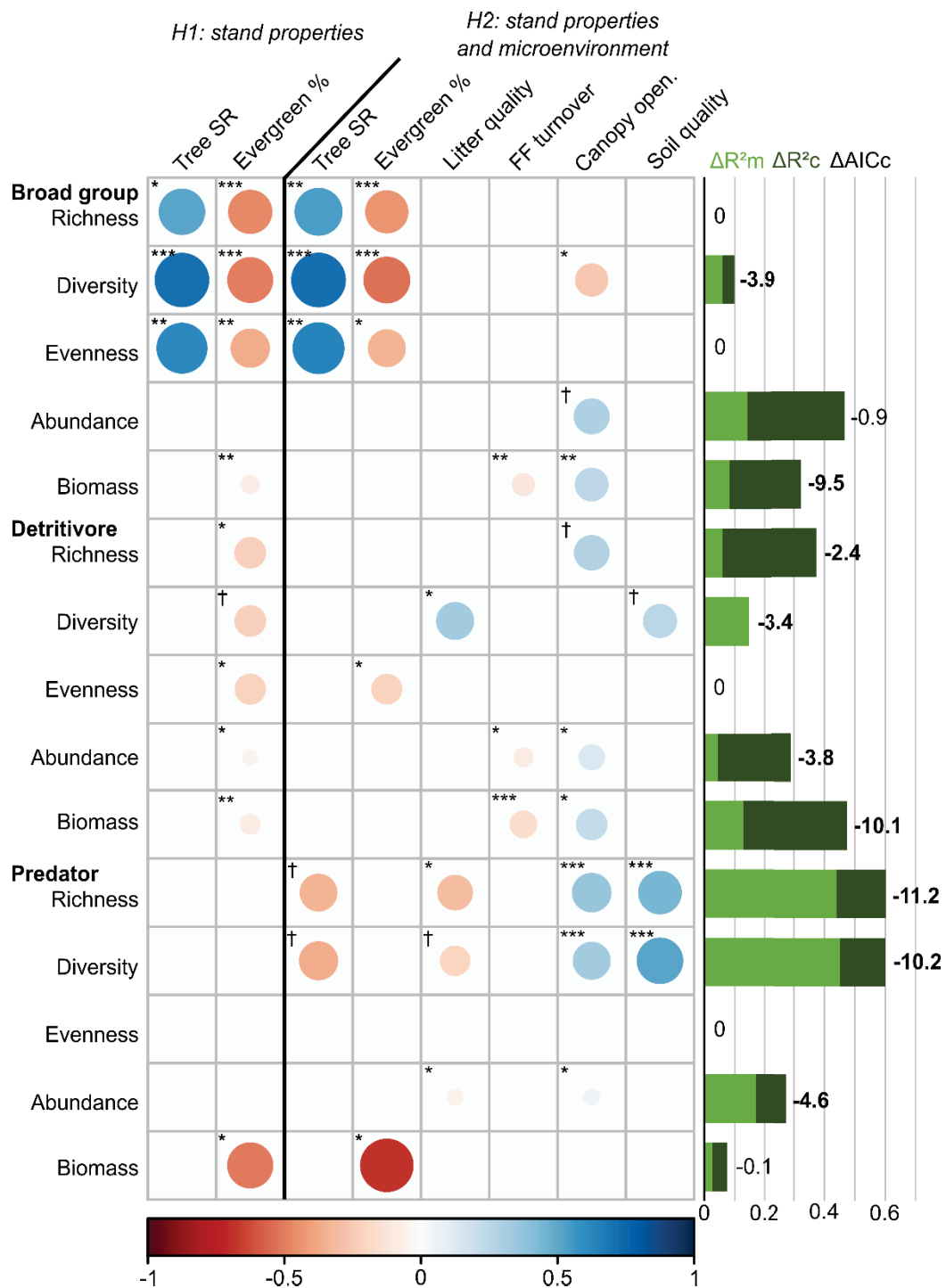


Figure 3.2 – Standardized estimates and explained variance from Multimodel Inference. Circle size and colour intensity are proportional to the effects strength, red colour show for negative effect, blue colour show positive effect). The level of significance of the effect is indicated (†, *, **, ***: p -value < 0.1, < 0.05, < 0.01, < 0.001). Non significant variable estimates are not shown but are reported in Table S5. The bar graph on the right indicates the change in the proportion of variance explained by fixed effects (R^2_m , light green) and fixed plus random effects (ΔR^2_c , dark green), as well as the difference in AICc (ΔAIC_c , number) between the most parsimonious models from each of the two hypotheses. Tree SR= tree species richness, FF mass= forest floor mass, Canopy open.= canopy openness.

2.3.2. Community structure

When all macrofauna was considered, the proportion of explained variance by fixed effects (R^2_m) in the full model (M2) varied from 14% (abundance) to 44% (Hill $_{q=1}$ ' diversity D_1). Accounting for random effects (R^2_c) increased the proportion of explained variance to 24% (evenness J) and to 76% (biomass), indicating a strong variability between countries. Broad group richness, Hill $_{q=1}$ diversity and evenness were well predicted in the reduced model (M1), while biomass, and to a lesser extent abundance, were better predicted in the complete model (M2). Broad group richness, Hill $_{q=1}$ diversity and evenness were higher in mixed than in monospecific stands (M1, S: std.est.= 0.51, $p= 0.013$; D_1 : std.est.= 0.72, $p < 0.001$; J: std.est.= 0.62, $p < 0.01$, Fig. 2, Fig. S2.5-S2.6), and at the same time decreased with the proportion of evergreen trees (M1, S: std.est.= -0.46, $p < 0.001$; D_1 : std.est.= -0.50, $p < 0.001$; J: std.est.= -0.36, $p < 0.01$, Fig. 2, Fig. S2.5-S2.6). There were no consequent changes between M1 and M2 in the proportion of explained variance or AICc, except for broad groups D_1 that also decreased with canopy openness ($\Delta AICc = -9.5$, $\Delta R^2_m = +0.06\%$, $\Delta R^2_c = +0.04\%$; Fig. 2, Table S2.5). Broad group abundance was poorly predicted regardless of the model, while biomass decreased with evergreen proportion in M1. However, this effect disappeared in M2, where total biomass instead decreased with forest floor mass and increased with canopy openness (Fig. 2.2). In this case, the best complete model showed a lower AICc ($\Delta AICc = -9.5$) and higher proportion of explained variance ($\Delta R^2_m = +0.08\%$, $\Delta R^2_c = +0.24\%$).

Regarding detritivore species assemblages, the proportion of variance explained by fixed effects was low, ranging from 4% (J) to 23% (biomass). Including the country as a random factor substantially increased the explained variance to 68% (J) and 79% (abundance), except for taxa Hill $_{q=1}$ ' diversity which only reached 24% of total explained variance in both models. In M1, none of the community metrics were affected by tree species richness, while evergreen proportion negatively affected all of them (Fig. 2.2, Table S2.5). However, most of these effects were replaced in M2 by the effect of microenvironmental variables, which produced a better model with substantially lower AICc and higher explained variance. Detritivore richness marginally increased with canopy openness, while detritivore Hill $_{q=1}$ ' diversity increased with litter quality (std.est.= 0.33, $p = 0.029$). Evergreen proportion was retained as the best predictor of detritivore evenness in both models (M1: std.est.= -0.22, $p = 0.012$; M2: std.est.=

-0.21, $p=0.033$; Fig. 2.2, Table S2.5). Forest floor mass was negatively correlated with abundance and biomass (ab: std.est.= -0.08, $p=0.013$; m: std.est.= -0.17, $p<0.001$; Fig. 2.2, Table S2.5), while the opposite pattern was found with canopy openness (ab: std.est.= 0.15, $p=0.023$; m: std.est.= 0.22, $p=0.02$; Fig. 2.2, Table S2.5).

Most descriptors of predator assemblages were well explained by fixed factor, except for evenness, with R^2m ranging from 9% (biomass) to 45% (D_1). The random factor accounted for a very small part of predator richness, diversity, or evenness, but consistently increased explained variance for abundance and biomass. Most of community metrics were better predicted in the complete model. Predator species richness and (marginally) Hill's diversity decreased with litter quality (S: std.est.= -0.29, $p=0.012$; D_1 : std.est.= -0.21, $p=0.059$) and strongly increased with canopy openness (S: std.est.= 0.36, $p<0.001$; D_1 : std.est.= 0.33, $p<0.001$) and soil quality (S: std.est.= 0.45, $p<0.001$; D_1 : std.est.= 0.51, $p<0.001$). Here, changes in the proportion of explained variance and AICc were very high (S: $\Delta R^2m=+0.44\%$, $\Delta R^2c=+0.16\%$, $\Delta AICc=-11.2$; S: $\Delta R^2m=+0.45\%$, $\Delta R^2c=+0.15\%$, $\Delta AICc=-10.2$; Fig. 2.2, Table S2.5). Predator abundance weakly decreased with litter quality and weakly increased with canopy openness, while biomass strongly decreased with evergreen proportion in both the reduced and complete models.

2.4. Discussion

The results of our study show the effect of tree diversity and functional type (i.e. stand evergreen proportion) on soil macrofauna communities and highlight the underlying mechanisms. Interestingly, we found that forest stands with a low evergreen tree proportion supported macrofauna communities with a higher numbers of broad groups that were also more diverse and evenly represented. In contrast, at a species-level taxonomic resolution, the effects of tree species richness and functional type were less pronounced. Instead, litter quality, microhabitat and microclimate became important drivers of both detritivore and predator assemblage structure, with trophic cascade effects potentially occurring between these two trophic groups.

2.4.1. Main axes of variability in soil macrofauna communities

The results of our redundancy analysis show that as much as 38.4% of the total variability in macrofauna communities, when described at a coarse taxonomic resolution, was explained by an opposition between two extreme of a gradient from pure deciduous to pure evergreen stands. This gradient is consistent with the classification of ecosystems along a productivity gradient (Wardle 2004), soil process domain (Desie et al. 2019), or the distinction between different humus types ranging from mull, i.e. “fast turnover” and “acquisitive strategy”, to moder and mor, i.e. “slow turnover” and “conservative strategy” (Ponge 2003; Zanella et al. 2011).

In fast cycling systems, deciduous trees provide high-quality litter and canopy openness over the year, allowing the establishment of an important understory vegetation, which produces litter rich in important nutrients such as calcium and nitrogen (Reich et al. 2005; Gilliam 2007; Augusto et al. 2015). This results in both a higher earthworm proportion in macrofauna communities and more diverse detritivore assemblages in general (Reich et al. 2005). Being more abundant and diverse, macrodetritivores are expected to further accelerate litter burial and decomposition, thus reducing the litter layer thickness at the soil surface (Hedde et al. 2010; Coulis et al. 2016b). Conversely, the decrease in earthworm relative abundance and detritivore diversity in evergreen dominated forests is a long known pattern that can be explained by the poor quality of litter inputs as well as the more acidic conditions of the forest floor (Reich et al. 2005; Ammer et al. 2006; Schelfhout et al. 2017). Such a decrease in macrodetritivore abundance is expected to be associated to lower bacterial activity, thicker forest floor layer, and the promotion of other groups of smaller detritivores such as Collembola (Scheu et al. 2003). This probably also explains the observed increase in predator relative abundance in stands with higher evergreen proportion, as this group could benefit simultaneously from the higher diversity and amount of microhabitats, and from the increased availability of mesofauna prey (Arpin et al. 1986; Kaspari and Yanoviak 2009).

2.4.2. Tree diversity and functional type direct versus indirect effects

In line with our first hypothesis, both our reduced and complete model showed a strong positive effect of tree species richness and a negative effect of evergreen proportion on the

richness, diversity, and evenness of macrofauna broad groups. This is globally congruent with the results of other studies, that described a higher diversity of soil organisms at a broad taxonomic level in mixed compared to pure evergreen forests (Scheu et al. 2003; Salamon et al. 2008). As mentioned previously, many environmental factors can differ between mixed and pure forests, including litter quality and trait diversity, microhabitat heterogeneity and quantity, canopy openness and soil quality (Scherer-Lorenzen et al. 2005), and most of them could indirectly explain tree effects on soil macrofauna communities. However, when included in a more detailed statistical model, none of the microenvironmental variables considered in our study were found to explain macrofauna community metrics at a broad level of taxonomic resolution, apart from canopy openness which had a weak negative effect on Hill_{q=1} diversity. This suggests that tree species richness and evergreen proportion effects on macrofauna broad groups could be related to other microenvironmental variables not included in our analysis, such as litter trait diversity or microhabitat heterogeneity. This would be in line with other studies that have emphasized the importance of litter chemical and physical trait variation, which may both determine resource diversity for detritivores and microhabitat quantity and diversity for invertebrates in general (Hansen and Coleman 1998).

At a finer level of taxonomic resolution, tree species richness no longer had a detectable effect on detritivore nor predator community descriptors, as indicated by our reduced model. Concomitantly, the negative effect of evergreen proportion on detritivore and predator assemblages produced by the reduced model was not retained in the complete model, except for detritivore evenness and predator biomass. Instead, our results revealed rather an indirect effect via resource quality, habitat volume, and microclimate. The lack of tree species richness effect on macrofauna assemblages at this level of taxonomic resolution, is congruent with similar studies focusing on earthworms or on detritivorous and predatory beetles (Schwarz et al. 2015; Chamagne et al. 2016; De Wandeler et al. 2018). Other studies did report a positive effect of tree species richness on spiders, saproxylic beetles, or earthworm richness, but differences in sampling protocols and study design can probably explain these apparently contradictory results (Chamagne et al. 2016; Ampoorter et al. 2019). Here, we also have to consider that our design only included two levels of tree species richness (monocultures and 3-species mixtures), which is different from a true species richness gradient. This might have

impeded the detection of a tree diversity effect, if it occurs at another level of the diversity gradient. The negative effect of evergreen proportion on detritivore evenness was consistent regardless of the model, suggesting a significant importance of diversity of litter traits or microhabitat, as already discussed for broad group diversity. The negative response of predator biomass to evergreen proportion, which was also highlighted by both modeling approaches, and the simultaneous lack of effect on their abundance, indicates that evergreen trees may drive the predator assemblages towards smaller body-sized taxa. This supports the previously discussed idea that soil fauna communities in evergreen-dominated stands are dominated by small detritivores (Collembola and Acari), representing a preferred prey for small body-sized predators.

Detritivore and predator communities also showed a strong response to canopy openness, with increased detritivore abundance and biomass and predator richness and diversity in more open forests. This can first be explained by the direct controls exerted by canopy openness on forest ground insolation, water availability, and temperature conditions (Prescott 2002), as well as their expected effects on ectotherm activity and on animals' ability to access resources (Turner et al. 1987; Kaspari et al. 2000; Salmon et al. 2008a). Secondly, canopy openness may increase light and water availability for understory plants, which can result in higher plant cover and diversity (Thomas et al. 1999). Detritivores will thus benefit from the nutrient-rich herbaceous plant leaf litter and roots, which may constitute an important and high-quality source of organic matter (Lavelle and Spain 2001; Gilliam 2007; Henneron et al. 2015). Finally, predators may also rely on understory vegetation which determines to a large extent the characteristics and heterogeneity of their microhabitat (Pakeman and Stockan 2014b).

2.4.3. Detritivore versus predator responses

A surprising result of our study is the fact that predator assemblages seem to be more sensitive to soil quality than detritivores. This predator response to soil quality may first be attributed to the fact that roughly half of them belonged to Chilopoda in our samples (Table S2), a group which is known to have at least partly endogenous behavior and is therefore sensitive to soil properties (Blackburn et al. 2002). Conversely, the absence of detritivores' response may be explained by three mechanisms. First, it is possible that other soil and forest floor properties

not included here, such as forest floor pH or litter phosphorus content, may be more important for detritivore communities (De Wandeler et al. 2016). Secondly, detritivore assemblages were composed of both endogeic groups (endogeic Lumbricidae) and epigeic groups (epigeic Lumbricidae, Diplopoda, and Isopoda). Epigeic taxa may show weaker response to soil characteristics than endogeic taxa which may have resulted in the absence of response (Scheu and Falca 2000; Henneron et al. 2015). Finally, soil characteristics and plot scores on the first PCA axis were strongly country specific (Table 1), and it is possible that by including country as a random factor in the models, captured part of soil characteristics variations was obscured. This is supported by the small proportion of variance explained by fixed effects (14% on average) compared to the random country variable (50% of explained variance) for detritivore assemblage descriptors,

In addition to the direct and indirect effects of tree diversity and functional type on macrofauna communities, trophic cascades may also have occurred between detritivore and predator assemblages, particularly because Lumbricidae, and to a lesser extent Diplopoda and Isopoda, represent potentially important preys for Chilopoda and Araneae (Scheu and Falca 2000). First, higher detritivore abundance and biomass in response to increased canopy openness may have enhanced predator diversity and richness through higher resource availability (Abrams 1995). Secondly, increased detritivore diversity in response to litter quality may have resulted in a more heterogeneous resource for predators, potentially decreasing prey-finding probability for the more specialized species (Root 1973), and resulting in the observed less rich, diverse and abundant predator assemblages. These mechanisms stress the importance of including trophic interactions when modeling soil macrofauna distribution in forests (Scheu et al. 2003; Salamon et al. 2008). To this end, it would also be interesting to include in future studies other sampling methods, such as pitfall traps, that could be more effective at sampling large, mobile predators such as Carabidae that may feed on large Lumbricidae.

2.4.4. Importance of taxonomic resolution

Given that the effect of tree species richness and evergreen proportion was detectable on whole macrofauna communities described at a low taxonomic resolution but no longer on detritivore or predator assemblages identified at the species level deserves particular

attention. Mixed deciduous-evergreen stands, with their intermediate position between two forest type extremes (“fast” pure deciduous, versus “slow” pure evergreen systems) may provide the necessary conditions for the co-existence of a high number of broad groups with contrasting ecological requirements (Fig. 1). This can also be explained by the fact, as mentioned previously, that mixed deciduous-evergreen forests produce a litter layer with larger chemical and physical trait variation, thus increasing resource diversity for detritivores and microhabitat features for invertebrates in general (Schuldt et al. 2008). The same does not apply when considering individual detritivores or predator species, because their narrower environmental preferences limit them to a more restricted part of the environmental gradient. This can explain why, at the species level, detritivores and predators were more sensitive to resources, habitat, and microclimate conditions than to tree species diversity and functional type (Fig. S4; Kaspari 2001).

The differences in response patterns highlighted by the use of different levels of taxonomic resolution also illustrate some important methodological issues. Indeed, approaches at low taxonomic resolution are often favored in studies of soil macrofauna, especially because they allow to bypass the taxonomic impediment that exists for many groups of soil invertebrates (Decaëns et al. 2010). The use of broad taxonomic levels makes it possible to consider the whole macrofauna community without reducing datasets to the best-known groups for which species-level identifications are possible. Taxa of higher rank also have wider geographic distributions, making comparisons easier between geographically distant sites. In our case, where sites harbor contrasting macrofauna species pools, the multiple pedoclimatic changes along latitude may be the major drivers of soil communities (De Wandeler et al. 2018). This is supported by the fact that the proportion of variance explained by random effects is larger when using species than when using broad group as fundamental taxonomic units (Table S5), as well as the small effect of the included predictor variables on detritivore and predator assemblage composition in the dbRDA analysis (Table S4, Fig. S4). Finally, datasets constructed at coarse levels of taxonomic resolution also by definition have fewer zeros than those constructed at species level, thus increasing the robustness and statistical power of analyses (Harrison et al. 2018a). However, a corollary of this is that they are also potentially less efficient at detecting subtle community responses to ecological gradients since the

distributions of higher rank taxa along these gradients are wider than those of the species that constitute them (Kaspari 2001). This stresses the importance of investigating community responses at different levels of taxonomic resolution.

2.5. Conclusion

Our study highlights the complexity of the direct and indirect mechanisms underlying the relationships between tree species diversity and composition and macrofauna communities. Mixed forest stands supported richer, more diverse and even macrofauna communities, at a broad level of taxonomic resolution. Compared to mixed stands, pure deciduous stands favored Lumbricidae and other macrodetritivore groups, while evergreen forests were dominated by predator taxa. Combined, these two results suggest that mixed forest stands offer resource, microhabitat, microclimate, and soil conditions suitable for a wide range of organisms of contrasting lifestyles. Future studies should incorporate if possible quantitative description of changes in litter or fine root trait diversity and habitat heterogeneity, as they can be of importance for soil macrofauna. Macrofauna response to tree species diversity and functional type was detectable almost only at a coarse level of taxonomic resolution, while macrofauna species rather responded to microenvironmental variables. This highlights the importance of combining different levels of taxonomic resolution in order to elucidate in a comprehensive way the complex tree-macrofauna relationships in forest ecosystems

Acknowledgments

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Supplementary Information

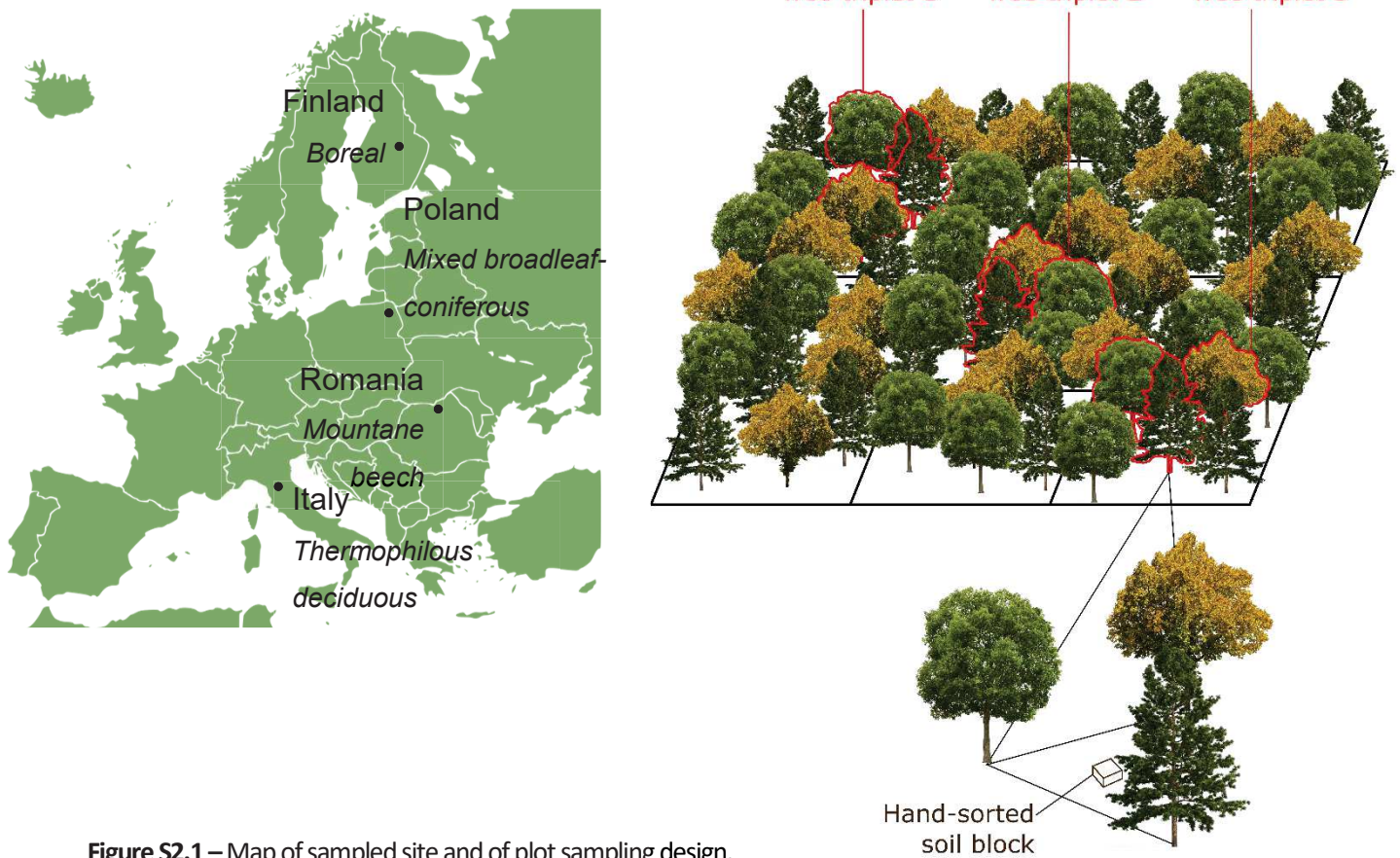


Figure S2.1 – Map of sampled site and of plot sampling design.

Appendix S2.1 – Protocol for predictor variables measurement describing soil, microenvironment and fresh litter traits.

Fresh leaf litter traits

Tree litter was collected from autumn 2012 to autumn 2013 at peak leaf litterfall depending on species-specific leaf fall. At the Italian, Romanian, and Polish sites, litter was collected using five suspended 0.5m² litter traps that were harvested every fortnight. At the Finnish site, freshly fallen leaf litter was collected from the forest floor.. The litter from the traps was air dried or dried in an oven at 38°C and pooled per plot. The foliar litter of the target tree species were sorted from the samples and weighed. A subsample was then dried at 65°C to constant weight. The ratio between dry mass at 65°C and the air-dried samples was used to calculate constant dried weight for all litter samples. Leaf litter was ground to obtain a uniform particle size of 1mm (Cyclotec Sample Mill, Tecator, Höganäs, Sweden). Total carbon and nitrogen concentrations were measured with a flash CHN Elemental Analyser (Flash EA 1112 Series, ThermoFinnigan, Milan, Italy). Cellulose and lignin content were determined using a fiber analyser (Fibersac 24, Ankom, Macedon, NJ, USA) according to the Van Soest extraction protocol (Van Soest and Wine 1967). Calcium (Ca) concentration was measured using an atom

absorption spectrometer (AAS, iCE 3000 series, ThermoScientific, China). To measure the concentration of polyphenols (i.e. total phenolics), 0.5g of ground litter was soaked in 30ml of 50% methanol, shaken for 2h, filtered (filter number 112, Durieux, Torcy, France), and then extracts were analysed spectrophotometrically using the Folin-Ciocalteu reagent using gallic acid as a standard. The 'Polyphenols' described in this study include every compound that contains a phenol unit, including, among other compounds, soluble phenolics, nonsoluble phenolics, condensed tannins, and hydrolysable tannins.

Microenvironment variables

At the same time as invertebrate sampling, four 15x15cm forest floor samples were collected down to the mineral soil, this included predominantly leaf litter but sometimes reproductive structures and small (<25mm diameter) branches. These samples were immediately air dried and then weighed to obtain litter mass (g.m^{-2}). All litter was collected down to the mineral soil, including reproductive structure and sometimes small branches (<25mm diameter). Understory vegetation biomass (g.m^{-2}) was estimated in 2012 from 3 subsamples per plot by clipping the vascular plant in a zone of 0.5x0.5m where understory vegetation was relatively abundant and the vegetation composition was representative of the whole plot. Non-woody organs were sorted, dried at 70°C, and then weighed and reported to the area sampled. Coarse woody debris (CWD, m^3) was measured over the entire plot including all standing dead trees and snags higher than 1,3m and thicker than 5cm DBH. Only CWD with its thicker end within plot borders were considered to be "in" the plot. Leaf Area Index value ($\text{m}^2.\text{m}^{-2}$) was estimated using a LAI 2000 Plant Canopy Analyzer (PCA, Li-Cor, Lincoln, NE, USA).

Soil variables

Soil variables are from the FunDivEUROPE project (Baeten et al., 2013) carried out in 2012 (cf. Ampoorter et al., 2019). After removing the forest floor, 9 mineral soil subsamples were taken using a 3.6cm diameter corer from 0 to 10cm depth and pooled. Samples were dried at 55°C, sieved to 2mm, and ground to a finer particle (Planetary Ball Mill PM 400 for 6 min at 280 rpm). Bulk density was then estimated from the dry soil weight divided by its volume (g.cm^3). Organic C and total N were analyzed with a Thermo Scientific FLASH 2000 soil CN analyzer (Italy) based on the dry combustion method (Matejovic, 1993). The organic C and total N concentrations were used to calculate mineral soil C/N ratios. The pH was measured in a 0.01M CaCl_2 solution at a ratio of 1:2.5 using 827 pH lab (Metrohm AG, Herisau, Switzerland). Soil texture was measured by laser granulometry (Malvern Mastersizer S) after pre-treatment for removal of organic material and carbonates if present (ISRIC and FAO (2002). Applied cut-off levels were: sand being from 0.63 to 2mm; loam from 2 μm to 0.63mm; clay under 2 μm .

Table S2.1 – Total abundance and biomass for each macrofauna group per trophic group at different scales.

Group	Total abundance (ind.)					Total biomass (g)				
	Finland	Poland	Romania	Italy	Europe	Finland	Poland	Romania	Italy	Europe
Detritivores	76	408	409	206	1099	14.1	69.7	103.8	14.6	202.1
Blattodea	2	0	0	4	6	0.03	0	0	0.03	0.06
Coleoptera										
coprophagous	0	0	61	0	61	0	0	34.4	0	34.4
Diplopoda	0	40	92	80	212	0.001	3.5	3.6	2.7	9.7
Diptera	28	88	25	39	180	0.7	3.7	1.9	0.3	6.6
Isopoda	0	3	44	62	109	0	0.04	0.5	1.6	2.2
Lumbricidae endogeic	10	99	157	1	267	3.6	40.4	57.3	0.03	101.3
Lumbricidae epigeic	24	119	25	14	182	7.9	18.5	4.8	6.5	37.8
Lumbricidae anecic	12	59	5	6	82	1.9	3.6	1.3	3.5	10.2
Predators	248	346	417	391	1402	0.8	5.8	2.5	3.0	12.1
Aranae	122	61	51	121	355	0.2	0.3	0.3	0.7	1.4
Chilopoda	17	47	226	148	438	0.1	0.4	1.4	1.9	3.8
Coleoptera predaceous	106	197	130	61	494	0.5	3.7	0.5	0.2	4.9
Dermaptera	0	35	10	0	45	0	1.4	0.4	0	1.7
Opiliones	3	6	0	61	70	0.01	0.1	0	0.3	0.3
Herbivores	77	169	74	130	450	1.3	6.3	4.2	2.5	14.3
Coleoptera rhizophagous	64	150	33	125	372	0.8	4.5	0.8	2.5	8.5
Gasteropoda	5	9	30	0	44	0.3	1.7	3.0	0	4.9
Lepidoptera	8	10	11	5	34	0.2	0.2	0.4	0.1	0.9
Total	401	923	900	727	2951	16.1	81.8	110.6	20.2	228.6

Table S2.2a – List of detritivore species with abbreviated name used in dbRDA biplots (Fig. S2.4), with abundance in each country and in Europe.

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
			145	159	200	5	504
Diplopoda			76	92	40	0	208
	<i>Brachydesmus superus</i>	B_sup	20	0	0	0	20
	<i>Chordeumatida sp</i>	Chord	3	0	0	0	3
	<i>Cylindroiulus apenninorum</i>	C_ape	33	0	0	0	33
	<i>Cylindroiulus burzenlandicus</i>	C_bur	0	6	0	0	6
	<i>Enantiulus transilvanicus</i>	E_tra	0	23	0	0	23
	<i>Glomeris connexa</i>	G_con	4	0	0	0	4
	<i>Glomeris tetrasticha</i>	G_tet	0	0	22	0	22
	<i>Julidae</i>	Julid	1	0	1	0	2
	<i>Julini</i>	Julini	0	6	0	0	6
	<i>Leptoiulus sp</i>	Lep_sp	0	2	3	0	5
	<i>Megaphyllum projectum</i>	M_pro	0	22	7	0	29
	<i>Ommatoiulus sabulosus</i>	O_sab	0	0	4	0	4
	<i>Ophiulus chilopogon</i>	O_chi	7	0	0	0	7
	<i>Polydemidae</i>	Polyd	0	1	0	0	1
	<i>Polydesmus burzenlandicus</i>	P_bur	0	4	0	0	4
	<i>Polydesmus complanatus</i>	P_com	0	0	3	0	3
	<i>Polydesmus sp</i>	Pol_sp	8	0	0	0	8
	<i>Unciger sp</i>	Unc_sp	0	10	0	0	10
	<i>Unciger transsilvanicus</i>	U_tra	0	1	0	0	1
	<i>Xestoiulus sp</i>	Xes_sp	0	17	0	0	17
Isopoda			62	44	3	0	109
	<i>Cylisticus gracilipennis</i>	C_gra	11	0	0	0	11
	<i>Philoscia affinis</i>	P_aff	36	0	0	0	36
	<i>Porcellio sp</i>	Por_sp	4	0	0	0	4
	<i>Porcellium conspersum</i>	P_con	0	0	1	0	1
	<i>Protracheoniscus politus</i>	P_pol	0	42	0	0	42
	<i>Sardoniscus verhoffi</i>	S_ver	1	0	0	0	1
	<i>Tiroloscia macchiae</i>	T_mac	10	0	0	0	10
	<i>Trachelipus rathkii</i>	T_rat	0	0	1	0	1
	<i>Trachelipus sp</i>	Tra_sp	0	0	1	0	1
	<i>Trichoniscidae sp</i>	Tricho	0	2	0	0	2

Table S2.2a – continued.

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
Lumbricidae			7	23	157	5	187
	<i>Allolobophora carpathica</i>	A_car	0	3	0	0	3
	<i>Allolobophora sturanyi dacidoides</i>	A_stu	0	5	0	0	5
	<i>Aporrectodea caliginosa</i>	A_cal	0	0	23	1	23
	<i>Aporrectodea rosea</i>	A_ros	0	1	2	0	3
	<i>Dendrobaena alpina alteclitellata</i>	D_alp	0	2	0	0	2
	<i>Dendrobaena attemsi</i>	D_att	0	1	0	0	1
	<i>Dendrobaena octaedra</i>	D_oct	0	3	27	0	30
	<i>Dendrobaena sp</i>	Dendr_sp	0	4	47	0	51
	<i>Fitzingeria platyura depressa</i>	F_pla	0	1	0	0	1
	<i>Lumbricus rubellus</i>	L_rub	0	0	16	0	16
	<i>Lumbricus sp</i>	Lum_sp	4	0	41	4	45
	<i>Lumbricus terrestris</i>	L_ter	0	0	1	0	1
	<i>Octodrilus complatus</i>	O_com	3	0	0	0	3
	<i>Octolasion lacteum</i>	O_lac	0	3	0	0	3

Table S2.2b – List of predator species with abbreviated name used in dbRDA biplots (Fig. S2.4), with abundance in each country and in Europe.

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
			271	277	113	139	800
Araneae			125	51	66	122	364
	<i>Agelenidae</i>	Agele	0	9	2	0	11
	<i>Agroeca sp</i>	Agr_sp	0	0	2	0	2
	<i>Agyneta cauta</i>	A_cau	0	0	0	1	1
	<i>Agyneta ramosa</i>	A_ram	0	0	0	2	2
	<i>Agyneta saxatilis</i>	A_sax	0	0	1	0	1
	<i>Alopecosa taeniata</i>	A_tae	0	0	0	1	1
	<i>Amaurobiidae</i>	Amaur	0	5	0	0	5
	<i>Araneae</i>	Aran	0	8	0	0	8
	<i>Areoncus humilis</i>	A_hum	0	0	1	0	1
	<i>Atypus sp</i>	Aty_sp	1	0	0	0	1
	<i>Ballus rufipes</i>	M_ruf	1	0	0	0	1
	<i>Ballus sp</i>	Ba_sp	0	2	0	0	2

Table S2.2b – continued

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
			271	277	113	139	800
Araneae			125	51	66	122	364
	<i>Callobius claustrarius</i>	C_cla	0	1	0	0	1
	<i>Centromerus arcanus</i>	C_arc	0	0	1	3	4
	<i>Centromerus isaii</i>	C_isa	1	0	0	0	1
	<i>Ceratinella brevis</i>	C_bre	0	0	2	0	2
	<i>Clubiana comta</i>	C_com	0	1	0	0	1
	<i>Clubiona terrestris</i>	C_ter	0	1	1	0	2
	<i>Clubionidae</i>	Club_sp	0	3	0	0	3
	<i>Clubiona sp</i>	Clun_sp	0	0	2	1	3
	<i>Cozyptila blackwalli</i>	C_bla	1	0	0	0	1
	<i>Dasumia taeniifera</i>	D_tae	3	0	0	0	3
	<i>Dictynidae</i>	Dic_sp	1	0	0	0	1
	<i>Dicymbium nigrum</i>	D_nig	0	0	0	1	1
	<i>Diplocentria bidentata</i>	D_bid	0	0	0	3	3
	<i>Diplocephalus latifrons</i>	D_lat	0	3	1	0	4
	<i>Diplocephalus picinus</i>	D_pic	0	0	2	0	2
	<i>Diplostyla concolor</i>	D_con	0	0	1	1	2
	<i>Dismodicus bifrons</i>	D_bif	0	0	0	1	1
	<i>Dyctina arundinacea</i>	D_aru	0	0	0	1	1
	<i>Dysderiidae</i>	Dysde	18	0	0	0	18
	<i>Enoplognatha ovata</i>	E_ova	0	0	1	0	1
	<i>Erigonella hiemalis</i>	E_hie	0	0	1	1	2
	<i>Euophrys frontalis</i>	E_fro	0	0	2	0	2
	<i>Euophrys sp</i>	Euo_sp	2	0	0	0	2
	<i>Gnaphosa sp</i>	Gna_sp	0	0	1	1	2
	<i>Gnaphosidae sp</i>	Gnaph	2	0	0	0	2
	<i>Gonatium rubellum</i>	G_rub	0	0	0	1	1
	<i>Hahnia ononidum</i>	H_ono	0	0	0	1	1
	<i>Hahnia pusilla</i>	H_pus	0	0	0	6	6
	<i>Linyphia hortensis</i>	L_hor	0	0	2	0	2
	<i>Linyphiidae</i>	Linyp	18	3	14	42	77
	<i>Liocranidae</i>	Liocr	0	5	0	0	5
	<i>Macrargus rufus</i>	M_ruf	0	0	1	1	2
	<i>Micrargus herbigradus</i>	M_her	0	0	0	1	1
	<i>Microneta viaria</i>	M_via	4	2	10	0	16
	<i>Minyriolus pusillus</i>	M_pus	0	0	0	6	6
	<i>Miturgidae</i>	Mit_sp	1	0	0	0	1

Table S2.2b – continued

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
Araneae	<i>Nemesia sp</i>	Nem_sp	2	0	0	0	2
	<i>Nemesiidae</i>	Nemes	6	0	0	0	6
	<i>Neon levis</i>	N_lev	1	0	0	0	1
	<i>Neon reticulatus</i>	N_ret	0	0	0	6	6
	<i>Neon sp</i>	Neon_sp	1	0	0	0	1
	<i>Neon valentulus</i>	N_val	1	0	0	0	1
	<i>Nerienne peltata</i>	N_pel	0	0	1	0	1
	<i>Oedothorax sp</i>	Oed_sp	0	1	0	0	1
	<i>Pardosa saltans</i>	P_sal	0	0	1	0	1
	<i>Pardosa sp</i>	Par_sp	0	0	2	2	4
	<i>Philodromidae</i>	Phil_1_sp	0	1	0	0	1
	<i>Philodromus sp</i>	Phil_2_sp	1	0	0	0	1
	<i>Phrurolithus sp</i>	Phr_sp	1	0	0	0	1
	<i>Pirata sp</i>	Pir_sp	0	1	4	0	5
	<i>Pocadicnemis pumila</i>	P_pum	0	0	0	1	1
	<i>Porrhomma pallidum</i>	P_pal	0	0	0	1	1
	<i>Robertus lividus</i>	R_liv	0	0	1	4	5
	<i>Robertus neglectus</i>	R_neg	0	4	0	0	4
	<i>Robertus scoticus</i>	R_sco	0	0	0	2	2
	<i>Robertus sp</i>	Rob_sp	0	0	0	3	3
	<i>Salticidae</i>	Salti	2	0	0	0	2
	<i>Tapinocyba insecta</i>	T_ins	0	0	9	7	16
	<i>Tapinocyba pallens</i>	T_pal	0	0	0	6	6
	<i>Tenuiphantes flavipes</i>	T fla	1	0	0	0	1
	<i>Tenuiphantes sp</i>	Ten_sp	18	0	0	0	18
	<i>Tenuiphantes tenebricola</i>	T_ten	14	0	0	2	16
	<i>Tenuiphantes zimmermanni</i>	T_zim	10	0	0	0	10
	<i>Theridiidae</i>	Theri	6	0	0	0	6
	<i>Theridion sp</i>	The_sp	0	1	0	0	1
	<i>Tibioloides arcuatus</i>	T_arc	0	0	0	4	4
	<i>Trachyzelotes sp</i>	Tra_sp	2	0	0	0	2
	<i>Walckenaeria alticeps</i>	W_alt	2	0	0	0	2
	<i>Walckenaeria dysderoides</i>	W_dys	0	0	0	2	2
	<i>Walckenaeria nodosa</i>	W_nod	0	0	0	1	1
	<i>Xysticus audax</i>	X_aud	0	0	0	1	1
	<i>Xysticus sp</i>	Xys_sp	0	0	0	2	2
	<i>Zelotibia sp</i>	Zel_sp	1	0	0	0	1
	<i>Zodarion italicum</i>	Z_ita	2	0	0	0	2
	<i>Zora nemoralis</i>	Z_nem	1	0	0	0	1
	<i>Zora sp</i>	Zora_sp	0	0	0	2	2
	<i>Zora spinimanna</i>	Z_spo	0	0	0	1	1

Table S2.2b - continued

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
Chilopoda			146	226	47	17	436
	<i>Arctogeophilus cf. macrocephalus</i>	A_mac	0	1	0	0	1
	<i>Chilopoda sp</i>	Chi_sp	1	0	0	0	1
	<i>Clinopodes flavidus</i>	C fla	11	0	0	0	11
	<i>Clinopodes rodnaensis</i>	C_rod	0	16	0	0	16
	<i>Clinopodes sp</i>	Cli_sp	7	6	0	0	13
	<i>Cryptops anomalans</i>	C_ano	1	0	0	0	1
	<i>Cryptops hortensis</i>	C_hor	2	0	0	0	2
	<i>Cryptops parisi</i>	C_par	7	12	0	0	19
	<i>Cryptops sp</i>	Cry_sp	0	1	0	0	1
	<i>Cryptops trisulcatus</i>	C_tri	1	0	0	0	1
	<i>Dignathodon microcephalus</i>	D_mic	1	0	0	0	1
	<i>Eupolybothrus sp</i>	Eup_sp	1	0	0	0	1
	<i>Geophilidae</i>	Geoph	4	2	0	0	6
	<i>Geophilus cf joyeuxi</i>	G_joy	40	0	0	0	40
	<i>Geophilus cf pygmaeus</i>	G_pyg	0	1	0	0	1
	<i>Geophilus cf studeri</i>	G_stu	0	6	0	0	6
	<i>Geophilus proximus</i>	G_pro	0	0	2	2	4
	<i>Geophilus richardi</i>	G_ric	1	0	0	0	1
	<i>Geophilus sp</i>	Geo_sp	7	3	0	0	10
	<i>Henia brevis</i>	H_bre	1	0	0	0	1
	<i>Henia vesuviana</i>	H_ves	9	0	0	0	9
	<i>Himantarium gabrielis</i>	H_gab	1	0	0	0	1
	<i>Lithobius blanchardi</i>	L_bla	6	0	0	0	6
	<i>Lithobius castaneus</i>	L_cas	1	0	0	0	1
	<i>Lithobius latro</i>	L_lat	0	14	0	0	14
	<i>Lithobius mutabilis</i>	L_muta	0	21	15	0	36
	<i>Lithobius muticus</i>	L_muti	0	5	0	0	5
	<i>Lithobius (Lithobius) sp</i>	L_L_sp	4	78	4	0	86
	<i>Lithobius tricuspis</i>	L_tri	1	0	0	0	1
	<i>Lithobius curtipes</i>	L_cur	0	0	20	13	33
	<i>Lithobius (Monotarsobius) sp</i>	L_M_sp	0	0	4	0	4
	<i>Lithobius (s l) sp</i>	Lit_sp	3	14	0	2	19
	<i>Lithobius burzenlandicus</i>	L_bur	0	21	0	0	21
	<i>Lithobius microps</i>	L_mic	4	0	0	0	4
	<i>Lithobius (Sigibius) sp</i>	L_S_sp	0	1	0	0	1

Table S2.2b – continued.

Class	Species name	Short name	Italy	Romania	Poland	Finland	Europe
Chilopoda	<i>Schendyla apenninorum</i>	S_ape	1	0	0	0	1
	<i>Schendyla carniolensis</i>	S_car	0	9	0	0	9
	<i>Schendyla nemorensis</i>	S_nem	0	0	2	0	2
	<i>Schendyla sp</i>	Sch_sp	0	3	0	0	3
	<i>Schendyla tyrolensis</i>	S_tyr	0	5	0	0	5
	<i>Schendyla vizzavonae</i>	S_viz	1	0	0	0	1
	<i>Stenotaenia cf. sorrentina / linearis</i>	S_sor.lin	1	0	0	0	1
	<i>Stenotaenia romana</i>	S_rom	5	0	0	0	5
	<i>Stenotaenia sp</i>	Str_sp	0	1	0	0	1
	<i>Stigmatogaster gracilis</i>	S_gra	22	0	0	0	22
	<i>Strigamia acuminata</i>	S_acu	0	5	0	0	5
	<i>Strigamia crassipes</i>	S_cra	2	1	0	0	3
Total abundance of identified detritivore and predator species			416	436	313	144	1304

Table S2.3 - Description of the predictor variables used in the study.

Variable code	Variable description	Units
<i>Stand properties</i>		
Tree S ¹	Plot tree species number; monospecific or three species mixture	number
Evergreen % ¹	Evergreen proportion of the total basal area	%
<i>Fresh leaf litter traits</i>		
Cellulose ²	CWM of the Cellulose content	%
Lignin ²	CWM of the Lignin content	%
Ca ²	CWM of the Calcium content	mg.g ⁻¹
N ²	CWM of the Nitrogen content	%
Polyphenols ²	CWM of the Total polyphenols content	%
<i>Microenvironnement</i>		
LAI ²	Leaf Area Index	m ² .m ⁻²
DWC_vol ²	Coarse deadwood volume	cm ² .m ⁻²
Litter_mass ¹	Forest floor litter mass	g.m ⁻²
Understory_mass ²	Understory herbaceous plant biomass	g.m ⁻²
<i>Soil quality (0-10cm depth)</i>		
BD ²	Bulk density	g.cm ⁻³
C ²	Carbon concentration (CaCl ₂)	mg.g ⁻¹
Clay ²	Percentage of clay per soil amount	%
CN ²	Carbon:nitrogen ratio	—
pH ²	pH CaCl ₂	—
<i>Constructed variables</i>		
Litter quality	Site PCA score on the first axis for litter trait CWM	—
Forest floor mass	Site PCA score on the first axis for microenvironment variables	—
Canopy openness	Site PCA score on the second axis for microenvironment variables	—
Soil quality	Site PCA score on the first axis for soil variables	—

¹ Data from SoilForEUROPE project

² Data from FunDivEUROPE project

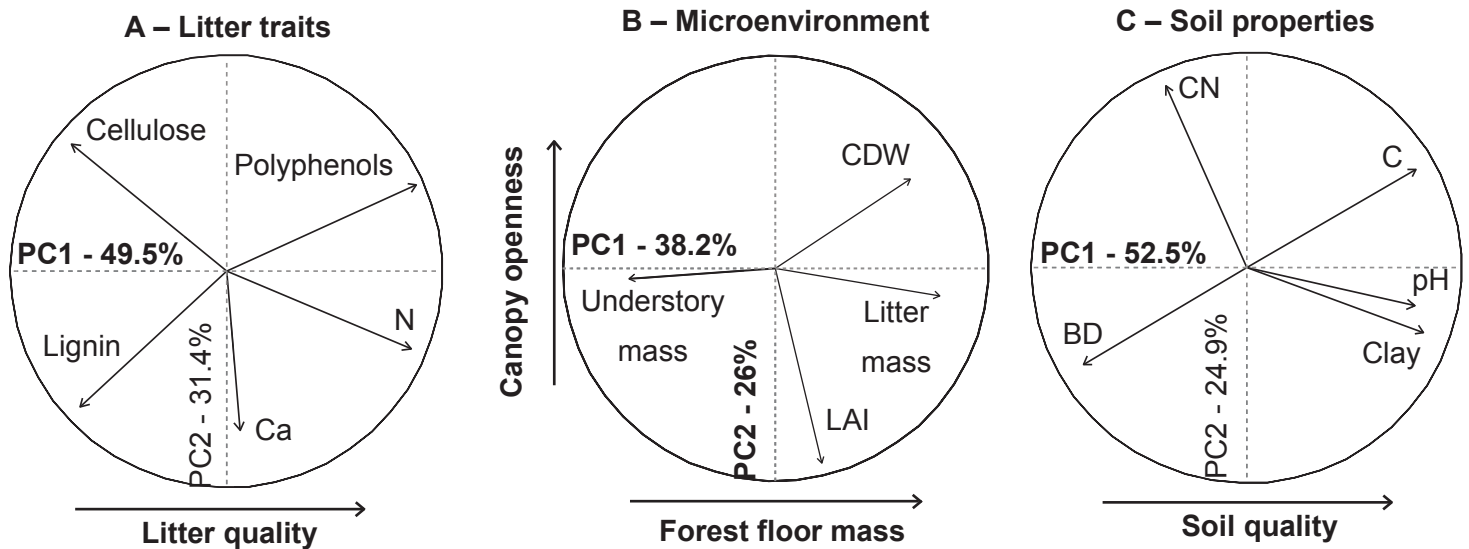


Figure S2.2 – Variable correlation circle on PCA axes 1 and 2 for **A-** fresh leaf litter CWMs, **B-** microenvironment variables, and **C-** soil properties. Abbreviations: N= nitrogen content, Lignin= lignin content, Cellulose= cellulose content, Polyphenols= polyphenols content, Ca= calcium content, Litter mass: mass of forest floor litter per unit ground area (g.m^{-2}), Understory mass = biomass of understory herbaceous vegetation per unit ground area (g.m^{-2}), CDW = coarse deadwood debris volume per unit ground area (g.m^{-2}), LAI: leaf area index $\text{m}^2.\text{m}^{-2}$, C= carbon content (mg.g^{-1}), CN= carbon to nitrogen ratio, pH= pH CaCl_2 , Clay= clay content, and BD= bulk density. All variables were scaled before running the PCA. The percentage of inertia explained by each axis is given. The interpretation of the axes is given for those which were retained as constructed explanatory variables in the dbRDA and MMA analyses (in bold).

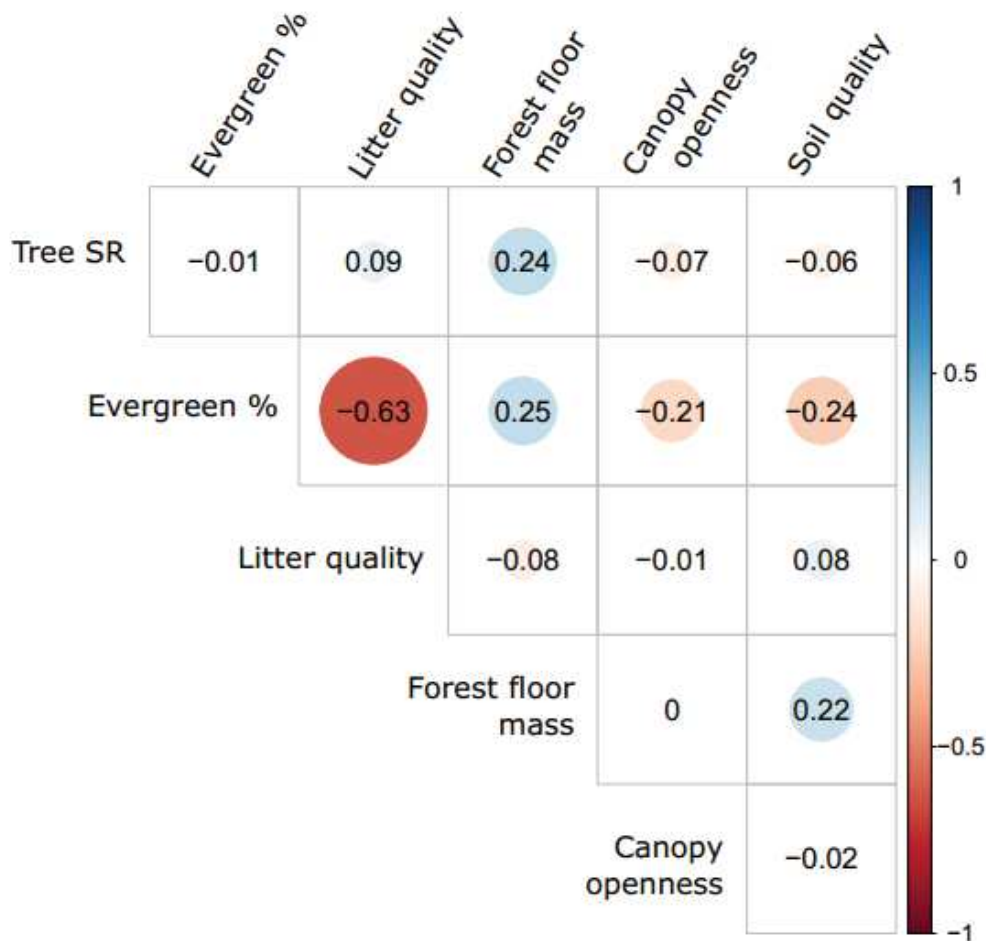


Figure S2.3 – Pearson correlation plot between predictor variable. Color indicates the direction of the correlation: negative (red) or positive (blue). The strength of the correlation is proportional to the color intensity and circle size. Variables explained in the legend of Table S1.

Table S2.4 – ANOVA table of the dbRDA ordination values of the all macrofauna, detritivore and predator assemblage dissimilarity matrices. The scores along the first two dbRDA axes, the Sum of Squares (SS), the Variance Inflation Factor (VIF), Fisher's statistics with degrees of freedom, and the p-value are shown for each predictor variable. Scores above 0.2 are in bold to indicate important predictor variables.

		<i>RDA axis 1</i>	<i>RDA axis 2</i>	<i>SS</i>	<i>VIF</i>	<i>F</i>	<i>Df</i>	<i>p value</i>
Ecogroups	<i>Proportion of variance</i>	38.4	23.4					
	<i>F</i>	3.97	2.41					
	<i>p-value</i>	<0.001 ^{***}	0.08 ⁺					
Predictor	Tree SR	0.16	- 0.34	0.14	1.1	0.95	1	0.6
	Evergreen %	0.59	0.61	0.30	2.2	2.00	1	<0.01**
	Litter quality	- 0.52	-0.13	0.36	3.6	2.40	1	<0.01**
	Forest floor mass	- 0.73	-0.03	0.25	2.3	1.67	1	0.04*
	Canopy openness	- 0.22	0.13	0.28	2.5	1.81	1	0.02*
	Soil quality	0.00	- 0.26	0.23	3.2	1.52	1	0.04*
Detritivore	<i>Proportion of variance</i>	31.4	18.9					
	<i>F_{1,44}</i>	2.18	1.31					
	<i>p-value</i>	0.13 ^{ns}	0.93 ^{ns}					
Predictor	Tree SR	-0.12	- 0.49	0.28	1.1	0.89	1	0.66
	Evergreen %	0.90	-0.01	0.52	2.2	1.64	1	0.03*
	Litter quality	- 0.59	0.55	0.52	4.2	1.63	1	0.04*
	Forest floor mass	-0.16	0.19	0.35	3.6	1.10	1	0.42
	Canopy openness	-0.19	0.21	0.19	3.5	0.58	1	0.96
	Soil quality	0.01	-0.09	0.35	3.1	1.10	1	0.33
Predators	<i>Proportion of variance</i>	33.2	19.7					
	<i>F_{1,53}</i>	2.36	1.4					
	<i>p-value</i>	0.06 ^{ns}	0.73 ^{ns}					
Predictor	Tree SR	-0.07	- 0.53	0.28	1.1	0.91	1	0.61
	Evergreen %	- 0.68	0.42	0.53	2.2	1.69	1	0.01*
	Litter quality	0.64	-0.05	0.41	3.6	1.30	1	0.14
	Forest floor mass	0.69	0.40	0.42	2.3	1.33	1	0.05*
	Canopy openness	0.09	- 0.30	0.24	2.5	0.77	1	0.83
	Soil quality	-0.02	0.14	0.30	3.2	0.96	1	0.41

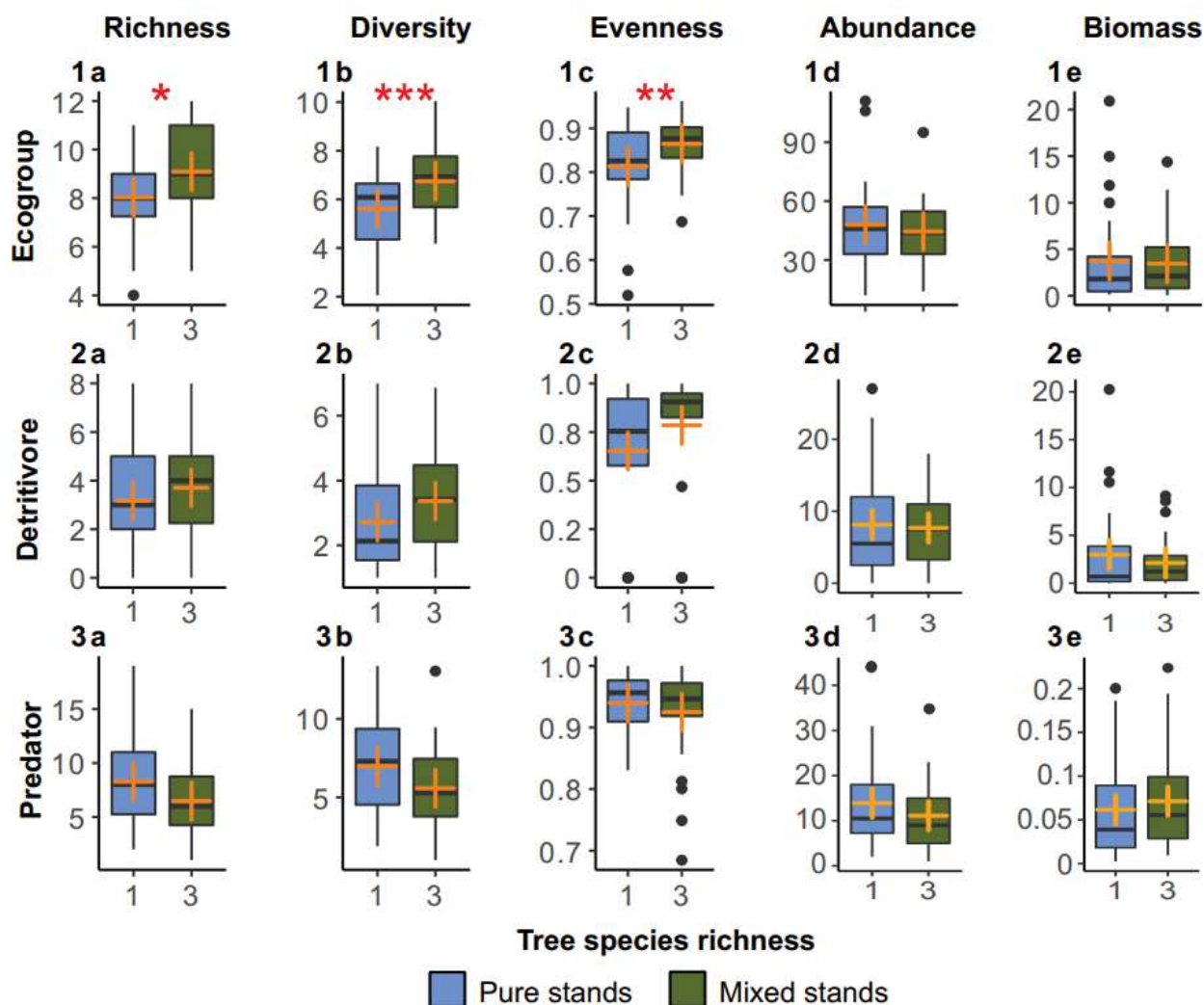


Figure S2.5 – Boxplot of the community descriptor, a: Richness, b: Hill_{q=1} Diversity, c: Pielou's Evenness, d: Abundance (number of individuals), and e: Biomass (g) for (1) the whole macrofauna community, (2) detritivore assemblage, and (3) predator assemblage. Significance level are indicated in red (*, **, ***: p -value < 0.05, < 0.01, < 0.001), obtained from the model averaging approach (see Material and Methods section). Orange plus signs indicate mean values. The blue boxes indicate pure stands and green boxes indicated mixed stands.

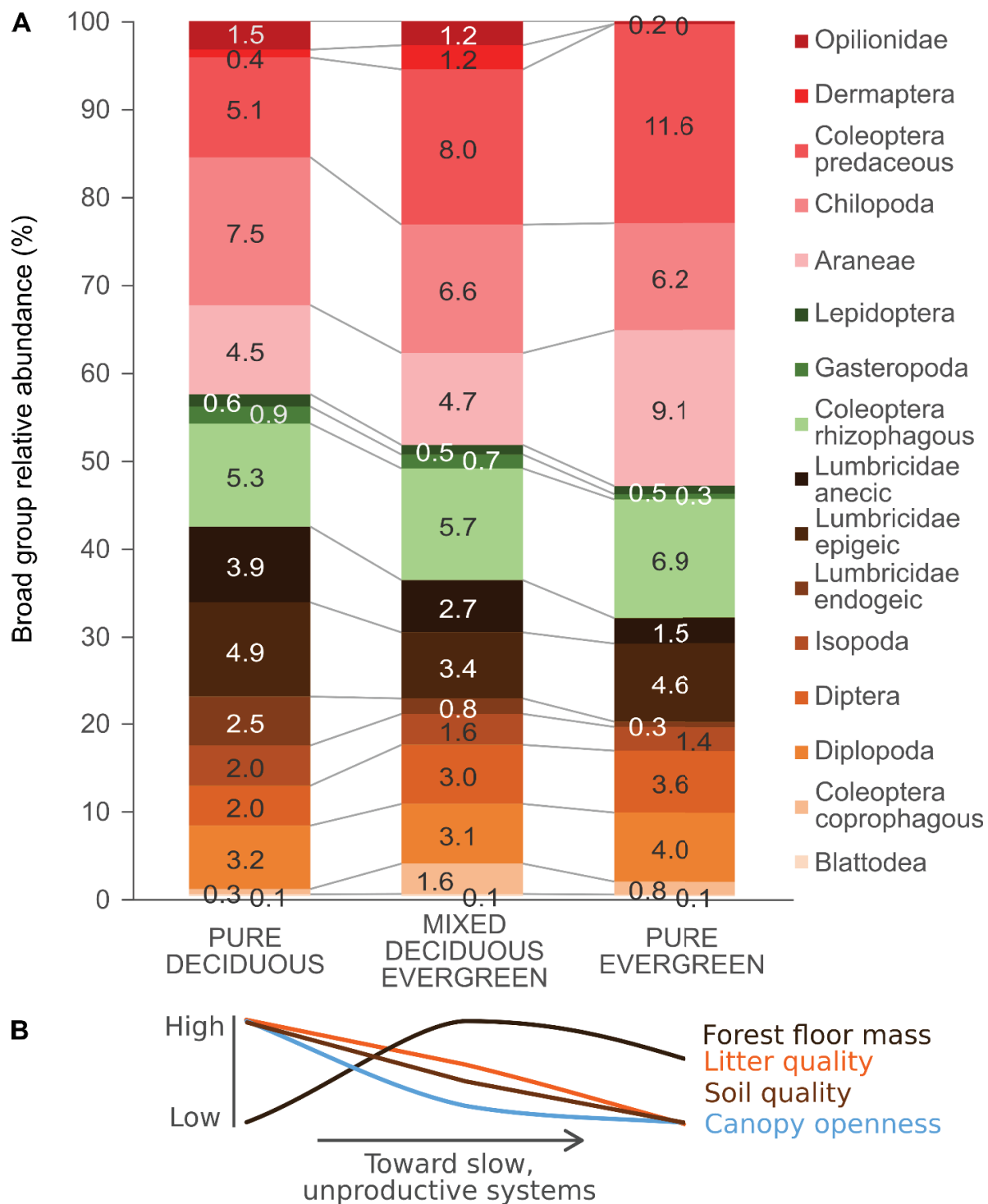


Figure S2.6— Changes in macrofauna community composition and microenvironmental variables in different forest stand types. “Deciduous” refers to stands only composed of deciduous tree species (pure or mixed), “Mixed deciduous-evergreen” refers to stands containing either 1 or 2 evergreen species among the three tree species, and “Evergreen” refers to stands only composed of evergreen trees (pure or mixed). **A)** Relative abundance of each broad groups; colors refer to trophic group (red= predator, green= herbivore, brown= detritivore). **B)** Changes in microenvironmental conditions. Curves were obtained by using mean plot PCA score (see Fig. S2 and the Material and Methods section for details) for each forest stand types.

Table S2.5 – Results of Multimodel Inference comparing the first and second hypotheses. The predictor variable standardized estimate with significance level (†, *, **, ***: p -value < 0.1, < 0.05, < 0.01, < 0.001) is shown for each response variable for each community descriptor (i.e. broad groups, detritivores, and predator). The highest proportion of explained variance and AICc are also indicated for each community descriptor best model. ΔR^2m , ΔR^2c , and $\Delta AICc$ are obtained by calculating the difference between the R^2m , R^2c and AICc of the best model including all predictors ($H2$) and of the best model with only the tree stand properties ($H1$). Tree SR= tree species richness, Evergreen %= evergreen proportion of basal area, FF mass= forest floor mass, S= richness, H= Diversity (Hills_{q=1}), J= evenness, ab= abundance, m= biomass

	H1: Stand properties					H2: Stand properties and microenvironment									H1 vs H2		
Community descriptor	Tree SR	Evergreen %	R ² m	R ² c	AICc	Tree SR	Evergreen %	Litter quality	FF mass	Canopy openness	Soil quality	R ² m	R ² c	AICc	ΔR ² m	ΔR ² c	ΔAICc
Broad groups																	
Richness	0,51 *	-0,46 ***	0,27	0,40	245,7	0,55 **	-0,44 ***	-0,02	-0,18	-0,12	0,05	0,27	0,40	245,7	0,00	0,00	0,0
Diversity	0,72 ***	-0,50 ***	0,38	0,40	217,2	0,72 ***	-0,52 ***	-0,04	-0,14	-0,25 *	0,09	0,44	0,44	213,2	0,06	0,04	-3,9
Evenness	0,62 **	-0,36 **	0,23	0,24	-143,2	0,65 **	-0,33 *	0,15	-0,11	-0,18	0,13	0,23	0,24	-143,2	0,00	0,00	0,0
Abundance	-0,20	-0,06	0,00	0,06	564,3	-0,17	0,10	0,23	-0,23	0,30 †	0,15	0,14	0,39	563,4	0,14	0,32	-0,9
Biomass	-0,03	-0,07 **	0,09	0,52	129,0	0,01	-0,02	0,11	-0,11 **	0,26 **	0,09	0,17	0,76	119,5	0,08	0,24	-9,5
Detritivore																	
Richness	0,07	-0,22 *	0,05	0,39	278,6	0,11	-0,11	0,26	-0,22	0,29 †	0,24	0,11	0,70	276,2	0,06	0,31	-2,4
Diversity	0,27	-0,23 †	0,05	0,24	249,3	0,30	-0,11	0,33 *	-0,01	0,17	0,27 †	0,20	0,24	245,9	0,15	0,00	-3,4
Evenness	0,20	-0,22 *	0,04	0,68	3,0	0,20	-0,21 *	-0,09	-0,10	0,14	0,17	0,04	0,68	3,0	0,00	0,00	0,0
Abundance	-0,04	-0,05 *	0,06	0,55	155,2	-0,02	-0,03	0,05	-0,08 *	0,15 *	0,05	0,10	0,79	151,4	0,04	0,24	-3,8
Biomass	-0,10	-0,09 **	0,11	0,38	141,6	-0,02	-0,08	0,13	-0,17 ***	0,22 *	0,14	0,23	0,73	131,6	0,13	0,35	-10,1
Predator																	
Richness	-0,27	-0,01	0,00	0,28	342,9	-0,33 †	-0,15	-0,29 *	0,06	0,36 ***	0,45 ***	0,44	0,44	331,7	0,44	0,16	-11,2
Diversity	-0,29	-0,01	0,00	0,30	307,9	-0,36 †	-0,18	-0,21 †	0,02	0,33 ***	0,51 ***	0,45	0,45	297,6	0,45	0,15	-10,2
Evenness	-0,32	0,05	0,00	0,11	-162,0	-0,32	0,13	0,13	-0,18	-0,32	0,20	0,00	0,11	-162,0	0,00	0,00	0,0
Abundance	0,00	0,00	0,00	0,37	115,9	-0,01	-0,02	-0,05 *	0,03	0,05 *	0,06	0,17	0,47	111,4	0,17	0,10	-4,6
Biomass	0,56	-0,50 *	0,07	0,34	-205,4	0,49	-0,69 *	-0,50	0,36	0,01	0,40	0,09	0,39	-205,5	0,03	0,05	-0,1

Chapter 2

Ecosystem scale environmental filtering of ground-beetle (Coleoptera: Carabidae) functional traits in European forests

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Abstract

The development of trait-based approaches allowed considerable progress on the understanding of how ecological communities assemble in response to various abiotic (environment or management) and biotic drivers (e.g. trophic interaction or mutualism). This framework can also help in describing how plant assemblage structure shape soil fauna communities. Ground beetles were sampled by pitfall and ecological preferences as well as morphological traits were measured for each species to describe communities' functional structure. RLQ and null model analyses were used to investigate carabid assemblage response to forest stand diversity and structure, soil and microhabitat properties, and resource availability. Forest canopy openness favored flying carabid with wider habitat and diet niche breadth while more packed canopy increased the proportion of apterous species, specialized to forest habitat. Changes in soil temperature and understory vegetation biomass and diversity due to variation in the amount of light reaching the ground are possible mechanisms to explain this effect. Evergreen proportion induced the reduction of carabid mean body mass as well as the reduction of functional dispersion, likely through the creation of less fertile systems. The use of functional traits was powerful in explaining plant-animal interaction and bring valuable insight to the assembly rules of ground beetles communities.

Keywords

Functional traits, null model, microclimate, microhabitat, biotic interaction

3.1. Introduction

Ground beetles (Coleoptera: Carabidae) represent one of the most diverse, abundant and widespread taxonomic group of predator invertebrates in the soils of most terrestrial ecosystems (Thiele 1977). Their large distribution along with their sensitivity to a number of natural and anthropogenic environmental factors make them a widely used bioindicator group for bio-monitoring, especially in agricultural and forests ecosystems (Rainio and Niemela 2003; Pearce and Venier 2006; Koivula 2011). They are described as opportunistic feeders but most species however exhibit feeding preferences, and can present mouthpart adaptations indicating trophic specialization e.g. for zoophagous or granivorous diets (Lindroth 1985; Laroche 1990). By selectively consuming other invertebrates or plant seeds, they may exert a strong top-down control on both soil invertebrates and vegetation, including a number of pest species (Weseloh 1985; Kanat and Özbolat 2006). By doing so, they potentially impact the composition and dynamics of invertebrate and plant communities, and therefore represent crucial actors of nutrient cycling (Schmitz et al. 2015). Their important biodiversity value and their role in ecosystem functioning stress the importance to understand the assembly dynamics of carabid communities and what are the factors shaping their functional structure.

Understanding community assembly processes is an old goal of ecology (Diamond 1975), which recently benefited from the development of trait-based approaches (Pakeman 2011; Mason and de Bello 2013). Traits are any morphological, phenological, morphological, physiological or behavioural characteristics that influence an individual performance in the ecosystem (Violle et al. 2007; Pey et al. 2014c). Two broad trait categories, i.e. response and effect traits, are usually distinguished. Response traits are features whose values in ecological communities are influenced by the biotic interactions and abiotic environment, and that can therefore be used to depict how different factors act as filters to sort species from the regional pool (Lavorel and Garnier 2002). The relative importance of species interactions and physical environment on community assembly can be detected by scrutinizing variations in trait mean values at the community level (i.e. CWM for community weighted mean; Garnier et al. 2004) or in trait diversity (Mouchet et al. 2010). Environmental filtering is for instance expected to reduce trait variability and to center CWM around the most suitable values in a given set of

environmental properties (Weiher and Keddy 1995; Keddy and Weiher 1999). On the opposite, interspecific competition may forbid the coexistence of species presenting similar traits related to resource uses, thus inducing an overdispersion of these traits as a consequence of limiting similarity (MacArthur and Levins 1967; Weiher and Keddy 1995). Recently, the use of null model (Gotelli 2000; Gotelli and Ellison 2002) has gained certain popularity to test for environmental filtering on functional structure of soil invertebrates communities (Pakeman and Stockan 2014a; Astor et al. 2014; Wong et al. 2019). Null models consist in a randomization of real data that produce community patterns expected in the absence of deterministic rules, which are compared to observed community patterns to track for non-randomness in their organization (Connor and Simberloff 1979; Gotelli 2001). For example, ground beetle functional diversity was shown to be lower than expected by chance with increasing land-use intensity (from woodland to crops), which was interpreted as a result of environmental filtering in the most intensive systems (Pakeman and Stockan 2014a). However, those studies applied to the soil biota remain scarce and limited to certain ecosystem types, hampering our understanding of assembly rules in ground beetle communities, especially in forest ecosystems (Wong et al. 2019).

In forest ecosystems, the majority of studies on ground beetle ecology investigated community responses to different forest management systems, forest age, and disturbance, classifying carabids in different groups according to their habitat specialization, diet, dispersion ability, and size (Kotze et al. 2011). These studies found that forest with more open canopy due to young forest age, clear-cut, or windthrow, harbor higher diversity and abundance of ground beetles, notably due to the presence of habitat generalist and flying species that tend to disappear during forest ageing and canopy closure (Niemela et al. 1993; Nagy 2016; Skłodowski 2017). This is explained by the low availability and complexity of litter and other microhabitat on which depend many species, including forest specialists, in the more open/disturbed stands (Niemelä et al. 1996; Antvogel and Bonn 2001), but also by the ability of small-bodied, flying, habitat generalist species to rapidly colonize these habitats and replace forest specialists (Skłodowski 2017). Prey abundance, which also depends on litter and microhabitat availability, can also affect carabid abundance, diversity, and proportion of zoophagous species (Guilemain et al. 1997). Forest stand productivity, either quantified

through soil quality (high organic matter, nitrogen, and clay content, pH close to neutrality; Bünemann et al. 2018), or inferred from evergreen proportion (Skłodowski 2002; Desie et al. 2019), thus may indirectly promote carabid abundance, diversity, and mean individual biomass via modulating prey availability (Skłodowski 2006; Oxbrough et al. 2010). Understory vegetation may also determine trophic resource availability for carabids whatever their feeding regime (i.e. omnivorous, zoophagous, granivorous or nectarivorous) together with providing them with microhabitats. Understory vegetation biomass and diversity was therefore shown to be a significant driving factor for carabid community structure (Butterfield 1997; Taboada et al. 2010; Pakeman and Stockan 2014a). The number of tree species composing forest canopy, as well as the identity of trees (in particular the proportion of evergreen and deciduous), are therefore expected to directly or indirectly affect carabid communities through modifying environmental features such litter inputs and quality, understory vegetation structure and composition, canopy cover and prey availability (Chapitre 1; Scherer-Lorenzen et al. 2005; Ampoorter et al. 2019; Jactel et al. 2020). However, this remains a blank research field as virtually no study has been carried out to date with an appropriate sampling design to disentangle the effects of tree species diversity and tree identity on ground beetle communities (Nadrowski et al. 2010).

In this chapter we sampled ground-beetle communities in 64 forest stands with different tree species richness (i.e. mono- versus tri-specific) and functional composition (i.e. with different proportions of evergreen versus deciduous), distributed along a latitudinal gradient in Europe. We used morphological traits to characterize the functional structure of carabid communities and we combined factorial and null model analyses to explore its relationships with different environmental factors describing tree stand structure, soil quality, and microhabitat and resource availability. We hypothesized that: *H1* – Tri-specific stands provide more diverse microhabitat and higher prey availability, leading to a higher functional diversity of carabid communities with an increased proportion of generalists species; *H2* – Stands with higher evergreen proportion negatively affect macrofauna and understory vegetation diversity, thus reducing carabids functional diversity while favoring small body sized zoophagous species; *H3*: Stands with closed canopy select forest specialist species that present a lower ability to fly (i.e. apterous or brachypterous species) and a better walking capacity (i.e. increased leg length);

H4: Forests on more fertile soil will present ground-beetle communities with a higher average body mass; *H5*: Stands with dense and diversified understory vegetation, provide more epigeic preys, thus favoring balanced feeding diets in carabid communities by increasing simultaneously the proportion of granivorous and zoophagous species.

3.2. Material and methods

3.2.1. Study sites and environmental variables

The sampling sites are the same 64 forest plots distributed in Italia, Romania, Poland and Finland as described in chapter 1. In each of them, 12 environmental variables were measured (see material and methods of Chapter 1 for detailed description of the methods) to describe specifically: 1) Ecosystem structure variables using tree species richness, evergreen proportion (percentage of the total stand basal area), leaf area index (LAI in $\text{m}^2.\text{m}^{-2}$), and understory vegetation biomass and species richness; 2) Local scale soil features, including physico-chemical soil properties (0-10cm organo-mineral layer) (i.e. C/N ratio, % of organic carbon, pH [H_2O], bulk density in $\text{g}.\text{cm}^{-3}$, and % of clay), forest floor litter mass, and biomass of potential prey. Understorey vegetation richness was included as a surrogate for microhabitat complexity. Potential prey consisted in the most abundant soft bodied macrofauna taxa (i.e. biomass of Lumbricidae, Gastropoda and Lepidoptera) that were collected by hand-sorting soil blocks as described in Chapter 1.

3.2.2. Ground beetle sampling and identification

Ground beetles were sampled in the 64 forest plots placing four pitfall traps in each of them, three of them being placed in the tree triplets where soil blocks were excavated, the fourth one in a random place distant of at least 20m from the three others. Each pitfall consisted in a plastic pot (95 mm diameter and 115 mm deep), filled with 70% ethanol, buried into the soil up to its top, and protected from rainfall, litter fall and mammals activity by a small metallic roof. Traps remained in the field for two consecutive weeks during the physiological spring of each study site. Collected individuals were sorted from plant debris that fell into the pots, and were preserved in clean 70% ethanol before being identified under a stereoscope using different identification keys (Trautner and Geigenmüller 1987; Hurka 1996; Coulon et al.

2011). Only specimen identified to the species level were kept in the analysis since the ecological preferences and traits are given at this taxonomic resolution. It is important to note here that this led to remove all individual of the *Amara* genus that represented 22.4% of the community. Identification to species level of these specimen will be soon done.

3.2.3. Trait selection, acquisition, and coding

We selected ecological preferences and traits among those currently used in trait-based approaches of terrestrial insects, and assuming that they would efficiently capture the main dimensions of species ecological niche and functions (Table 1): body mass, leg length (metafemora length), affinity for forest habitat, diversity of habitat used, degree of zoophagy (diet composed of living animal items), diversity of diet, and wing morphology. Body mass was measured on all individuals by weighing them to the nearest 0.1 mg after gently drying them with a soft tissue. Metafemora length was measured on at least 5 individuals collected on different sites and different sex when possible (some species were captured less than five times and there was a majority of males in the samples). It was then reported to the individual total length (i.e. the distance from the apex of elytra to the apex of mouth parts). Allometric equation between individual total length and leg length and body mass were used to infer leg length on the individuals that were weighed but not measured. Species ecological preferences were extracted from the online database BETSI (Biological and Ecological Traits of Soil organisms; Pey et al. 2014a). The BETSI database documents information on ecological preferences and traits mined from different sources such as aggregated data, identification keys, books, etc. The information obtained from each source is coded in the database using fuzzy coding with traits decomposed into modalities to which species are associated by an affinity score. The affinity (ranging from 0 to 3) is then transformed into a percentage to build the trait profile for each species². The fuzzy coding approach has the advantage to numerically code textual information and to conserve intraspecific trait variability. Practically, the

² For example, in Hurka 1996, it is reported that *Harpalus atratus* is brachypterous, rarely macropterous. This relates to the species wing morphology. In this case *H. atratus* will be given the affinity 3 to the attribute “brachypterous”, and the affinity 1 to “macropterous”. See a detailed description of fuzzy coding adapted to soil invertebrates in (Hedde et al. 2012).

ecological preference “diet” had several attributes in BETSI database and only categories specific to ground beetles were kept (zoophagous, phytophagous, and necrophagous). The affinity for each of these modalities was used to calculate the diet diversity of each species with the Shannon diversity index (Shannon 1948). The affinity for “zoophagous” attribute was used to quantify species degree of zoophagy. The same procedure was applied to calculated species habitat breadth (i.e. Shannon index of habitat used by a species) and species degree of specialization for forest habitat, using “habitat preference” regrouped into five modalities (wetland, open habitat, forest, shrub heathland, urban green space). Wing morphology was decomposed in a binary way, species being assigned either to “non functional wings” (i.e. “apterous” and “brachypterous”) or to “macropterous” species that are actually able to flying. Species list with trait value is given in Table S1.

Table 1 – List of ecological preferences and traits used in the analyses to describe ground beetles ecological niche and functions.

Trait / Ecological preference	Organism function	Value	Reference
Body mass ¹	Metabolism, reproduction, mobility, diet, and microhabitat	Numerical (mg)	Peters 1993; Barton et al. 2011
Leg length/ total length ¹	Mobility, diet and microhabitat	Numerical between 0 and 1	Ribera et al. 1999; Kaspari and Weiser 2007; Barton et al. 2011; Hedde et al. 2015
Wing morphology ²	Mobility	Affinity for macropterous modality	Lindroth 1985; Venn 2016
Habitat diversity ²	Habitat niche	Continuous	Magura 2017
Forest affinity ²	Habitat niche	0 to 1	
Diet diversity ²	Diet niche	Continuous	Hedde et al. 2012
Degree of zoophagy ²	Diet niche	0 to 1	

¹ traits obtained by direct measurement on at least 5 individuals per species when possible,
² informations obtained from the BETSI database.

3.2.4. Statistic analyses

The dataset therefore consisted of 1) a table L providing the abundance of the 44 ground beetle species (in columns) for each of the 52 sampling plots (i.e. those remaining after removing the sites in which no ground beetle was found); 2) a table Q describing the 44 species (in rows; after removing *Amara* for which no species level assignment was achieved) using the 7 functional traits (in columns; list provided in Table 1); 3) a table R describing the 52 sampling plots using the 12 environmental variables.

The three tables were analyzed using RLQ analyses, a multivariate approach which maximizes the covariance between linear combinations of traits and environmental variables mediated by the species abundances (Dolédéc et al. 1996). This was done using the 'ade4' (Chessel et al. 2004; Dray et al. 2007) and the 'vegan' (Oksanen et al. 2019) packages for R. In order to explore the more comprehensively possible the links between traits and environmental factors, we computed three different RLQs with three partitions of the environmental table: in a first step the R table analyzed while keeping it whole, then it was split into two sub-tables, the first containing only the ecosystem structure variables, the second the local variables of soil. Each RLQ was performed after computing individual factorial analyses of the R, L and Q tables: 1) The L table was processed with correspondence analysis ('dudi.coa' function of 'ade4') on the data previously Hellinger transformed ('decostand' function of 'vegan'; Legendre and Gallagher 2001); 2) the R and Q tables were processed using principal component analyses ('dudi.pca' of 'ade4'). Then we used the 'rlq' function of the 'ade4' package to perform the double inertia analysis of the trait and environmental tables with a link expressed by the community table. The overall significance of the analysis, the links between traits and environmental variables and their association with the axes of covariation were tested through a fourth-corner analysis using the functions 'fourthcorner', 'fourthcorner2' and 'fourthcorner.rlq' (Legendre et al. 1997; Dray and Legendre 2008).

For each individual species assemblage, we calculated the observed specific richness (i.e. the cumulative number of species observed in the samples of a sampling plot). We then calculated the community weighted mean (CWM; Garnier et al. 2004b) of each of the functional trait used in the RLQs, as well as the functional dispersion (FDis), which is the abundance-weighted average distance of species to the centroid of the functional space (Villéger et al. 2008). This

was done using the 'dbFD' function of the 'FD' package for R (Laliberté et al. 2014). A null model approach was then used to explicitly analyze the assembly rules involved in the trait - environment relationships as highlighted by the RLQs. We first generated 999 randomized communities using the 'randomizeMatrix' function and the 'independentswap' null model (Gotelli 2000) of the 'picante' package (Kembel et al. 2020). Then we calculated the standardised effect size (SES) as suggested by (Gotelli and McCabe 2002):

$$SES = (I_{obs} - I_{sim}) / \sigma_{sim}$$

where I_{obs} is the observed index, I_{sim} is the mean of the 999 indices obtained from the simulated communities and σ_{sim} is the standard deviation of the 999 indices from the simulated communities. Positive SES values greater than 2.0 represent competition between species for nonrandom patterns of co-occurrence (i.e. segregation), while SES values below -2.0 represent cooperation between species for nonrandom patterns of co-occurrence (i.e. aggregation).

Variations of observed species richness, and of the SES of functional dispersion and trait CWM along the gradient described by the RLQ axes were tested using linear mixed-effects models (LMM) with country as random effect. LMM were fitted and analyzed using the 'lmer' function of the 'lme4' package (Bates et al. 2015), and p values were calculated with the 'lmerTest' package (Kuznetsova et al. 2017).

3.3. Results

In total, 2069 individuals were identified, belonging to 45 species and 16 genus. Thirty three of these species were found in a single country, eight occurred in 2 countries, and four in three countries (*Carabus cancellatus*, *Notiophilus palustris*, *Pterostichus niger*, and *P. oblongopunctatus*). The community was largely dominated by *P. oblongopunctatus* (943 individuals, 45.7%) and individuals of the *Amara* genus (462 ind., 22.4%) (Figure S1). 9 species were macropterous, notably *P. oblongopunctatus* and *Calosoma inquisitor* (20 individuals). 21 and 19 species could be categorized as forest and zoophagous specialist respectively (affinity > 75%).

The RLQs computed with the complete R table and with the soil variables only were found to be only marginally significant ($p = 0.065$ and $p = 0.111$), even if certain traits on the one hand, and certain environmental variables on the other hand, appeared to be significantly associated with the axes of these analyses (SI Fig 1 & 2). On the contrary, the RLQ using the variables describing the structure of the forest ecosystem appeared globally significant (fourth corner analysis $p = 0.042$), with both the link between species distribution and environment, and between species distribution and traits, being significant ($p = 0.001$ and 0.028 , respectively).

The two first axis of this RLQ explained 70% and 23% of the co-structure between tables R and Q (Fig. 1C). Axis 1 opposes: a) sites with high LAI (i.e. negative scores on RLQ1) hosting ground beetle assemblages characterized by species with high specialization for forest ecosystems, zoophagous diet, and low dispersal ability (brachyptery), to b) sites with more open vegetation (lower LAI; positive scores on RLQ1) where ground beetle communities tend to be composed of more generalist species (higher S_{hab} , lower proportion of forest and zoophagous species) with higher dispersal ability (macroptery) (Figs. 1A & 1B). On this axis, the ellipses corresponding to each country were rather overlapping, with a slight opposition between Romania (with forest ecosystems showing a higher LAI) and Finland (with more open forest ecosystems).

The second axis was mainly explained by the proportion of evergreen species in the forest composition. Sites with high proportion of evergreen species (positive scores on RLQ2) presented ground beetle assemblages composed by smaller species (lower body weight). However, it should be specified here that the contributions to RLQ2 of both the % of evergreens and the body mass are only marginally significant here (p values around 0.1).

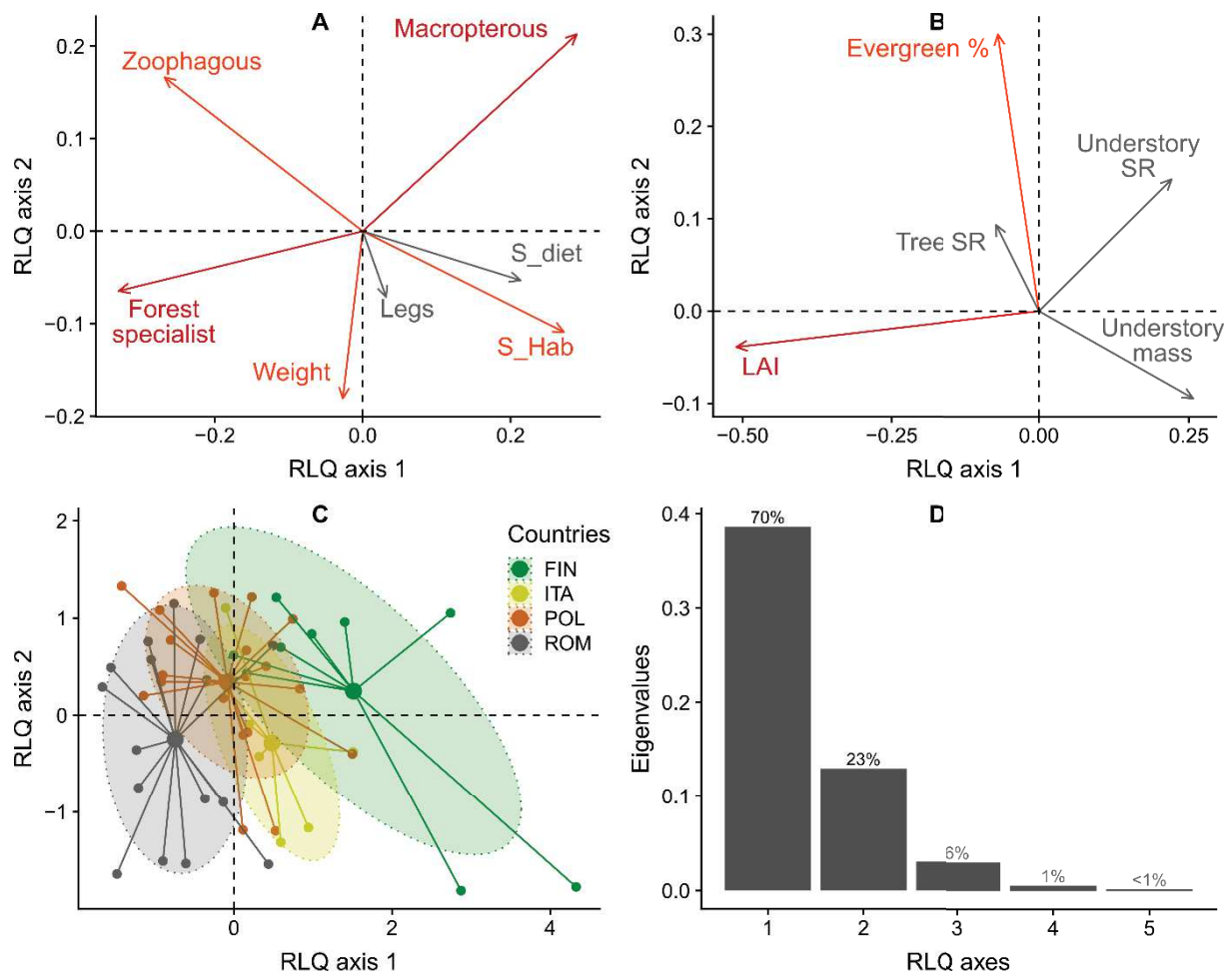


Figure 1. Results of the RLQ analysis using the ecosystem structure variables as R table: (A) Ordination of the functional traits of the first two axes of RLQ; (B) Ordination of environmental variables on the first two axes of RLQ; (C) Ordination of the individual communities clustered by countries on the first two axes of RLQ; (D) Eigenvalue diagram showing the % of overall variance explained by each axis. Red and orange arrows on figures (A) and (B) indicates traits or environmental variables significantly and marginally linked with RLQ axes ($p < 0.05$ and $0.05 < p < 0.1$, respectively); codes for traits in (A) as in Table 1; SR = species richness, LAI = leaf area index, FIN = Finland, ITA = Italy, POL = Poland, ROM = Romania.

Using the LMM approach with country used as a random factor, we found a significant correlation between observed species richness and RLQ1 and RLQ2, but the slope of the linear models adjusted on the cloud of points appeared to be almost flat (Figs. 2A & 2B). Functional dispersion decrease along RLQ2, with significantly lower values found in sites with higher % of evergreen trees (Fig. 2C). Despite being highlighted by the RLQ, the proportion of forest specialists and of macropetrous species in ground beetle assemblages was not anymore significantly correlated with RLQ1 when considering countries as a random factor in the LMM (SI Fig. 3G-H and 3K-L). RLQ1 was significantly positively correlated with the SES of habitat and trophic niche breadths (Figs. 2D & 2H) and with the proportion of zoophagous species (Fig. 2F). It is interesting to point out here that using country as a random factor in the LMM brings out the S_{diet} as responding significantly to RLQ1, whereas this was not the case in the fourth corner analysis. RLQ2 was significantly correlated with the habitat specialization (Fig. 2E), the proportion of zoophagous (Fig. 2G) species and species body weight (Fig. 2I). We found underdispersion in 10 communities for SES of FDis, five for SES of habitat niche breadth, and two for SES of proportion of zoophagous species. Overdispersion was observed in three communities for SES of habitat and diet niche breadth, and five for SES of body weight.

Overall, this shows that more open forest ecosystems have more generalists in their ground beetle assemblages (both in terms of habitat and trophic resources uses), and that species there also tend to be more frequently granivorous (lower proportion of zoophagous) with macropetrous wing morphology. Additionally, forests with a higher proportion of evergreen trees have ground beetle assemblages with lower functional dispersion, and tending to be characterised by smaller species with a higher proportion of habitat specialists and zoophagous taxa compared to pure deciduous ecosystems.

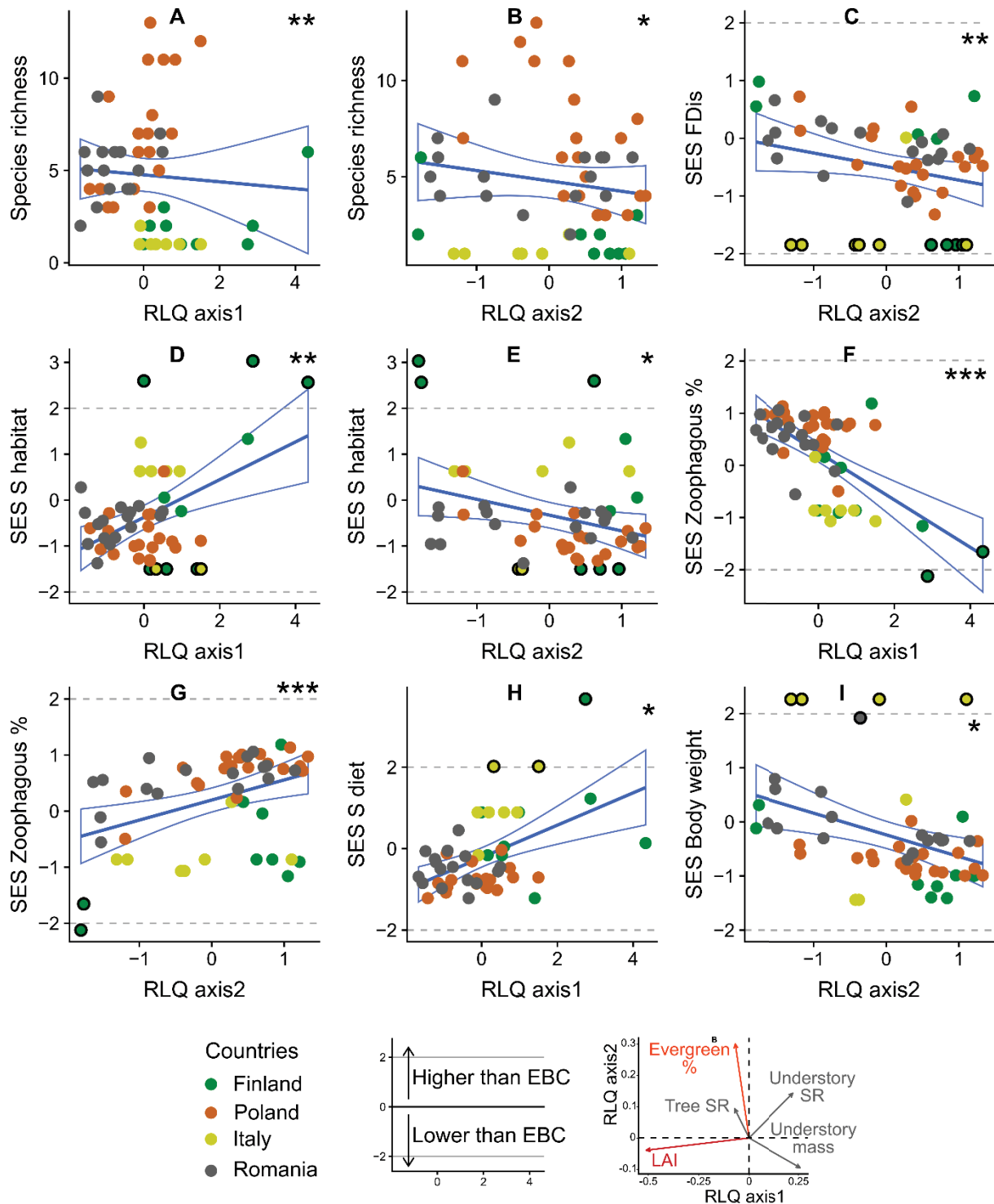


Figure 2. Significant correlations between the community scores on the first two axes of the RLQ and their taxonomic and functional diversity: (A-B) observed species richness on RLQ1 and RLQ2, (C) SES of functional dispersion on RLQ2, (D-E) SES of the diversity of habitat used on RLQ1 and RLQ2, (F-G) SES of the proportion of zoophagous species on RLQ1 and RLQ2, (H) SES of trophic niche breadth on RLQ1, (I) SES of body weight on RLQ2. The horizontal dashed lines indicate standardized effect sizes of -2.0 and 2.0, and points with bold contours indicate SES value >1.55 or <-1.55 (Astor et al., 2014).

Significance codes for linear mixed-effect models: 0 '****' 0.001 '***' 0.01 '**' 0.05. EBC = expected by chance.

3.4. Discussion

Across 64 forest stands in contrasted pedo-climatic contexts, ground beetle community functional structure was strongly structured by tree stand properties, in particular by canopy openness which had the highest contribution of the first axis of the RLQ, and to a lower extent by evergreen proportion in forest stands (second axis of the RLQ). We found no relationship between tree species richness and trait composition of carabids communities, which refuted our first hypothesis, but is congruent with other studies comparing pure and mixed coniferous/broadleaf forests (Oxbrough et al. 2010; Barsoum et al. 2014). Soil parameters as well as forest floor litter mass and potential prey biomass did not affect community functional structure in a significant way. Further null model analysis including country as random factor allowed to detect additional significant variations of the CWM of some traits or ecological preferences along the ecological gradients summarized by the two first RLQ axes, shedding some light on the mechanisms driving trait over and underdispersion.

3.4.1. Canopy openness drives most of carabid functional structure changes

The observed change in carabid functional structure in more open forest is in agreement with other studies reporting higher proportion of flying, small-bodied, habitat generalist species in more open forest stands (Niemela et al. 1993; Nagy 2016; Skłodowski 2017). These studies were investigating canopy gaps due to clear cutting or windthrow disturbance that induced many changes in the ground habitat, and substantially higher canopy openness than just naturally occurring as in our study. Accordingly to our third hypothesis, our study supports the fact that ground beetle communities show a strong sensitivity to canopy structure (Jukes et al. 2001; Vandegehuchte et al. 2015; Spake et al. 2016). Soil invertebrates can be highly sensitive to canopy openness as the amount of light reaching the forest floor greatly conditions ground temperature (Prescott 2002) and therefore the activity and ability of ectothermic organisms to access to their resource (Turner et al. 1987; Kaspari et al. 2000; Salmon et al. 2008b). In a 50 years-old common garden experiment with 13 tree species (eight deciduous and five evergreen trees), light availability was the strongest predictor of ground

beetle richness (positive relationship), while the nine other soil fauna groups sampled showed a smaller if not no response at all (Mueller et al. 2016). In our case, canopy openness effect on species richness, was not clear despite being significant, suggesting that the change in functional structure comes from changes in community composition rather than from variation of species numbers. Likely, from closed to open forests, non-flying forest specialists are progressively replaced by small-bodied flying species with large habitat breadths (Butterfield 1997; Skłodowski 2017). Sites with open canopy were also characterized by an important biomass and species richness of the understory vegetation, and although these environmental variables were not significantly correlated with any of RLQ axes, understory structure may have influenced carabid community composition (Brose 2003). Indeed, ground beetles may use understory vegetation as an habitat and a resource provider (i.e. plant seeds and nectar for granivorous species, or phytophagous preys for zoophagous species) (Butterfield 1997; Taboada et al. 2010; Pakeman and Stockan 2014a). This is supported in our study by the higher proportion of carabid species with wider diet and habitat niche breadth. Here, the inclusion of individuals of *Amara* genus would be interesting as this group usually is classified as phytophagous with important granivory (Laroche 1990) and generally have fully functional wings (Ribera et al. 1999). Further identification of specimen to species level and attribution of trait value is mandatory to confirm these assumptions.

3.4.2. Tree functional type rather than diversity affect carabid body size structure

On the second RLQ axis, evergreen proportion tended to affect carabid functional structure by reducing mean individual bodymass and functional dispersion, which is in agreement with our second and forth hypothesis. The few body size SES values that appeared to be higher than expected by chance originated from Italian sites where the large-bodied *Percus paykullii* species dominated the community, sometimes being the only species collected. Given that the first axis captured changes in carabid communities associated with canopy openness and understory vegetation, it is likely that evergreen effect acted through different mechanisms. Evergreen tree can induce strong changes in soil quality and fertility, notably through acidification and the production of a thick layer of recalcitrant litter (Reich et al. 2005; Augusto et al. 2015), that are known to affect carabid communities (Antvogel and Bonn 2001; Magura et al. 2003, 2005; Skłodowski et al. 2018). However, soil parameters and carabid traits were

not significantly linked according to the RLQ analysis when restricted to local soil variables. Since soil parameters were measured in the first 10cm of mineral soil, we did not have a proper description of forest floor quality that, although being linked, differ from mineral soil in its structure, density, and pH (Gobat et al. 2010). In one of the sampled site (Białowieża forests, Poland), Skłodowski (2002) reported the same increase in mean individual biomass with forest stand fertility and litter layer quality. Although not significant, forest floor mass, which is higher in unproductive sites, was always correlated with evergreen proportion in the soil and total RLQ analyses. Litter mass and proportion of needle is really important for carabid species (Niemela et al. 1992; Koivula et al. 1999; Magura et al. 2003; Skłodowski et al. 2018), and may explain the filtering of small species, able to move through the denser litter layer litter composed of needles (Hansen and Coleman 1998; Hättenschwiler et al. 2005a). Additionally, less productive site may provide less favorable conditions for larval development as well as resource availability for larvae and adults, leading to lower capacity of the system to support large-bodied species (Abrams 1995; Szyszko et al. 2000; Aava-Olsson 2001; Skłodowski 2002). Finally, reduced body size may also reflect changes in resource availability since we observed more zoophagous carabids in evergreen dominated stands. As we find no significant relationship between the biomass of soft-bodied macrofauna and carabid traits, actual carabid resource may have been badly represented by our variable (Guillemain et al. 1997). In evergreen dominated stands, fungi dominates the microbial communities over bacteria, which benefit to the mesofauna such as springtails (Collembola) (Arpin et al. 1986; Salamon et al. 2008). Small-size zoophagous *Notiophilus* species that feed on collembola may therefore have increased in dominance in evergreen dominated stands. This change in predator bodymass is congruent with the response of other groups of predators such as spiders and centipedes which were collected in the same study sites by hand-sorting soil core (Chapitre 1). Future acquisition of information on collembola communities (Henneron and Berg, personal communication) will allow us to test this assumption.

3.3.3. Filtering of functional and taxonomic diversity

The decrease in species richness was clearer along the second than the first axis of the RLQ, and parallel the decrease in functional dispersion along this evergreen dominance gradient. Decreased species diversity in evergreen-dominated stands have already been reported in

other studies (Niemela et al. 1992; Magura et al. 2005; Skłodowski 2017). In our results, the decrease in functional dispersion observed with increasing evergreen proportion suggests that this change in canopy composition represents a significant environmental filter resulting in a decrease of trait dispersion within carabid communities. Functional characteristics of the vegetation were better predictor than taxonomy of the carabids community, especially of its functional structure. We finally highlight that trait-based approach was more efficient than studying taxonomic diversity for highlighting the interactions between vegetation structure and the assembly of ground beetle communities as recently shown by other studies comparing carabid communities in grasslands and forests (Pakeman and Stockan 2014a; Magura 2017).

3.5. Conclusion

Tree stand canopy openness and tree functional type induced strong filtering of carabid community functional structure, notably on the habitat and trophic resource niche breadth, wing morphology, and body mass. Our study therefore confirms the high sensitivity of ground beetles to environmental changes that make them interesting species that can be used as indicators to track the consequences of changes in canopy structure and community composition.

Supplementary information

Table S3.1 - Ground beetle species list with occurrence in each country (Finland, Poland, Romania, and Italy), abundance (ab), total relative proportion (%), weight (g), metafemora to total length ratio (leg); flight capacity (Macropterous), affinity for forest habitat (Forest specialist), diversity of used habitat (S_Hab), affinity for zoophagous diet (Zoophagous), and diversity of diet (S_diet). na indicate missing value in the BETSI database.

Species	Fin	Pol	Rom	Ita	ab	%	Weight	Leg	Macropterous	Forest specialist	S_Hab	Zoophagous	S_Diet
<i>Abax parallelus</i>		+	+		68	3,3	0,178	na	0	100,0	0,00	100,0	0,0
<i>A. parallelepipedus</i>		+	+		40	1,9	0,302	3,88	0	91,7	0,29	78,7	0,6
<i>A. schueppeli</i>			+		15	0,7	0,487	3,65	0	76,9	1,27	na	na
<i>Agonum fuliginosum</i>	+				1	0,0	0,013	4,95	0	0,0	1,33	na	na
<i>Anisodactylus hispanus</i>		+			5	0,2	0,063	3,44	1	0,0	0,00	na	na
<i>A. nemorivagus</i>		+			1	0,0	0,054	3,73	na	0,0	0,00	na	na
<i>Calathus mollis</i>	+				8	0,4	0,023	4,07	0	0,0	0,00	na	na
<i>Calosoma inquisitor</i>		+			20	1,0	0,335	4,48	1	100,0	0,51	100,0	0,0
<i>Carabus arcensis</i>		+			4	0,2	0,221	4,04	0	50,0	1,04	51,9	0,9
<i>C. auronitens</i>			+		7	0,3	0,543	5,51	0	100,0	0,54	60,0	1,0
<i>C. cancellatus</i>	+	+	+		65	3,2	0,542	4,92	0	50,0	0,69	83,3	0,5
<i>C. convexus</i>		+			8	0,4	0,453	4,46	0	100,0	0,61	50,0	0,7
<i>C. coriaceus</i>			+		2	0,1	2,309	4,97	0	100,0	0,00	81,0	0,7
<i>C. glabratus</i>			+		3	0,1	0,847	4,63	0	100,0	0,44	80,6	0,6
<i>C. granulatus</i>		+			2	0,1	0,321	na	1	25,0	1,39	83,6	0,6
<i>C. hortensis</i>		+			2	0,1	0,709	5,62	na	100,0	0,00	62,2	0,9
<i>C. linnaei</i>			+		9	0,4	0,320	6,14	na	100,0	0,00	0,0	0,0
<i>C. nemoralis</i>	+	+			43	2,1	0,650	4,31	0	80,0	0,50	69,5	0,8
<i>C. obsoletus</i>			+		3	0,1	0,662	5,00	0	100,0	0,00	80,0	0,5
<i>C. scabriusculus</i>		+			1	0,0	0,409	4,69	na	33,3	0,64	79,2	0,6
<i>C. violaceus</i>			+		2	0,1	1,087	5,53	0	69,0	0,96	100,0	0,0
<i>Harpalus latus</i>		+			3	0,1	0,048	3,04	1	66,7	0,64	0,0	0,0
<i>H. quadripunctatus</i>		+			2	0,1	0,050	2,86	na	na	na	na	na
<i>Leistus rufomarginatus</i>		+			2	0,1	0,029	5,55	0	100,0	0,98	100,0	0,0
<i>Limodromus assimilis</i>		+			4	0,2	0,059	4,51	1	37,5	1,73	100,0	na
<i>Loricera pilicornis</i>		+			1	0,0	0,014	5,95	1	100,0	0,00	94,4	0,2
<i>Molops piceus</i>			+		104	5,0	0,089	3,34	0	100,0	0,54	100,0	0,0
<i>Nebria brevicolis</i>		+			3	0,1	0,078	4,97	1	33,3	1,10	93,9	0,2
<i>Notiophilus palustris</i>	+	+		+	16	0,8	0,006	4,17	0	33,3	1,10	100,0	0,0
<i>Notiophilus rufipes</i>		+		+	4	0,2	0,006	3,51	0	100,0	0,00	71,4	0,6
<i>Percus paykulli</i>				+	12	0,6	0,551	3,48	na	50,0	0,69	na	na
<i>Pterostichus aethiops</i>		+			2	0,1	0,093	3,28	0	70,0	0,61	na	na
<i>P. anthracinus</i>		+			23	1,1	0,060	3,68	0	20,0	1,33	100,0	0,0
<i>P. burmeisteri</i>		+			3	0,1	0,066	3,66	0	100,0	0,66	100,0	0,0
<i>P. hagenbachii</i>		+			56	2,7	0,053	5,07	na	na	na	na	na
<i>P. jurinei</i>			+		1	0,0	0,084	3,68	0	100,0	0,00	50,0	0,7
<i>P. macer</i>		+			1	0,0	0,012	4,18	1	0,0	0,69	60,0	1,0
<i>P. melanarius</i>	+	+			67	3,2	0,168	3,35	0	30,0	2,03	45,9	0,0
<i>P. negligens</i>	+	+			17	0,8	0,011	3,95	0	14,3	0,41	na	na
<i>P. niger</i>	+	+	+		10	0,5	0,232	4,47	0	62,5	0,92	70,3	0,9
<i>P. oblongopunctatus</i>	+	+	+		943	45,7	0,073	3,76	1	100,0	0,00	100,0	0,0
<i>P. selmanni</i>			+		2	0,1	0,193	3,09	0	100,0	0,69	na	na
<i>Pterostichus strenuus</i>		+	+		14	0,7	0,010	3,60	0	60,0	0,95	71,4	0,6
<i>Trichotichnus laevicollis</i>		+			1	0,0	0,485	2,97	0	100,0	0,00	0,0	0,7

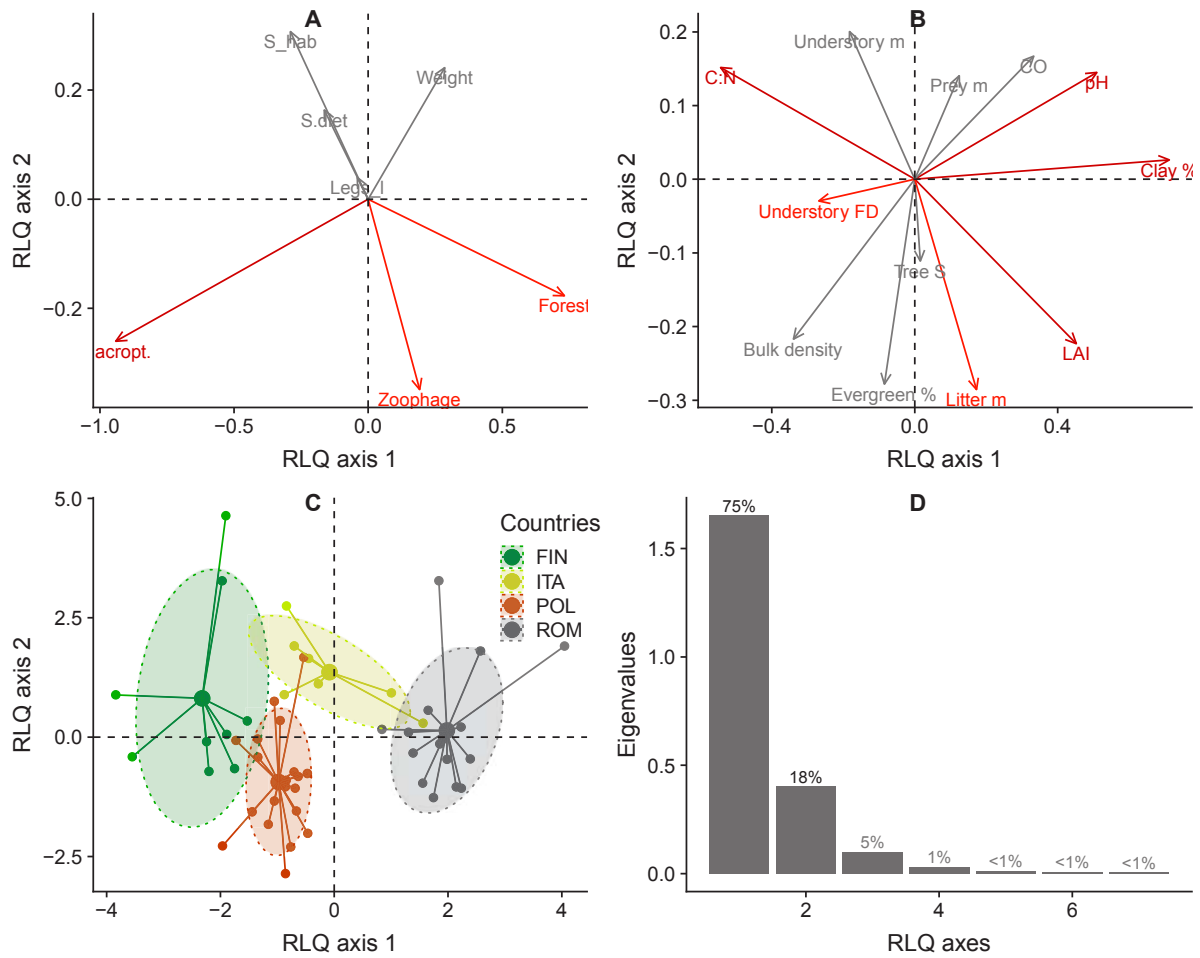


Figure S3.1. Results of the RLQ analysis using the complete R table: (A) Ordination of the functional traits of the first two axes of RLQ; (B) Ordination of environmental variables on the first two axes of RLQ; (C) Ordination of the individual communities clustered by countries on the first two axes of RLQ; (D) Eigenvalue diagram showing the % of overall variance explained by each axis. Red and orange arrows on figures (A) and (B) indicates traits or environmental variables significantly and marginally linked with RLQ axes ($p < 0.05$ and $0.05 < p < 0.1$, respectively).

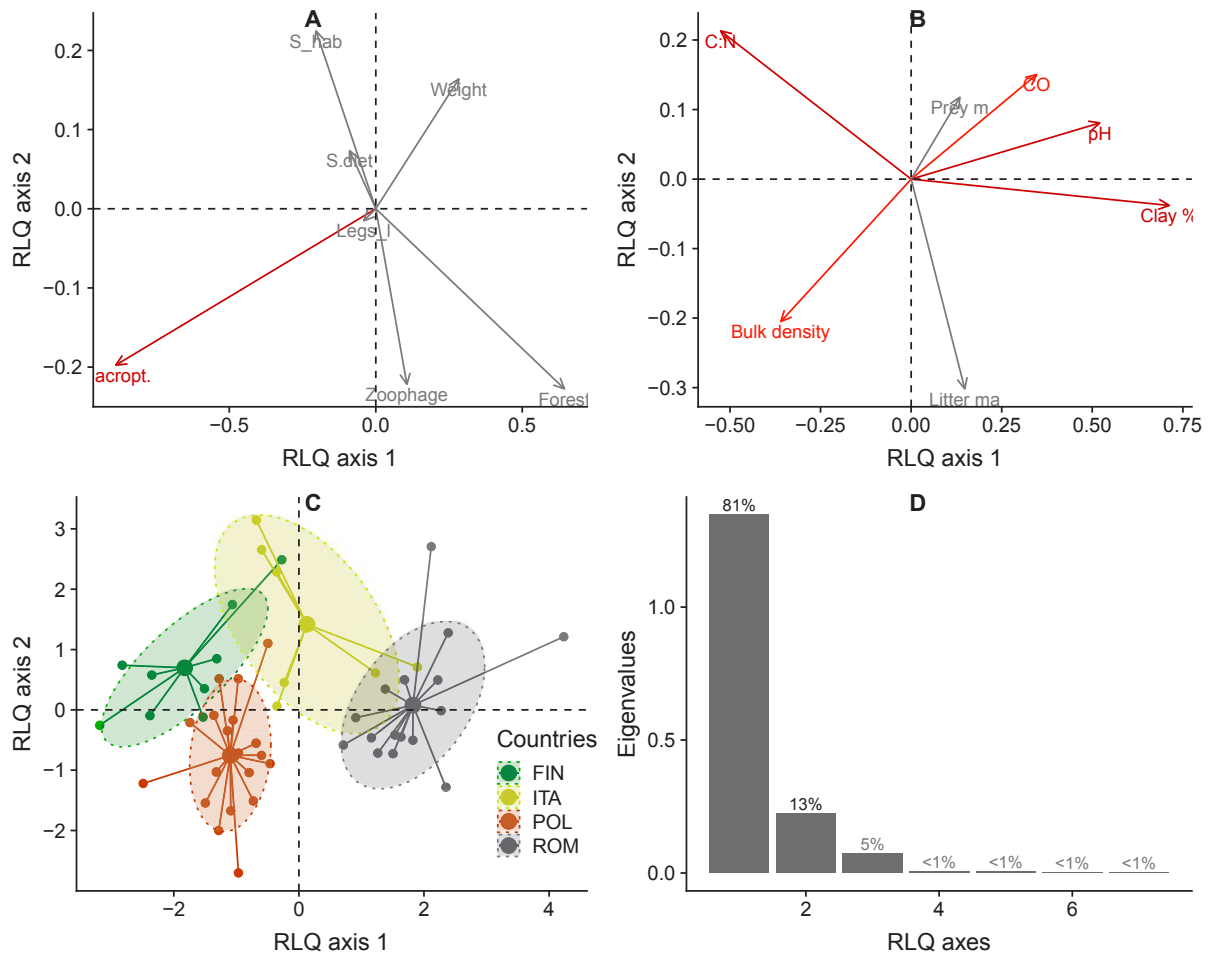


Figure S3.2 - Results of the RLQ analysis using the local soil variables as R table: (A) Ordination of the functional traits of the first two axes of RLQ; (B) Ordination of environmental variables on the first two axes of RLQ; (C) Ordination of the individual communities clustered by countries on the first two axes of RLQ; (D) Eigenvalue diagram showing the % of overall variance explained by each axis. Red and orange arrows on figures (A) and (B) indicates traits or environmental variables significantly and marginally linked with RLQ axes ($p < 0.05$ and $0.05 < p < 0.1$, respectively).

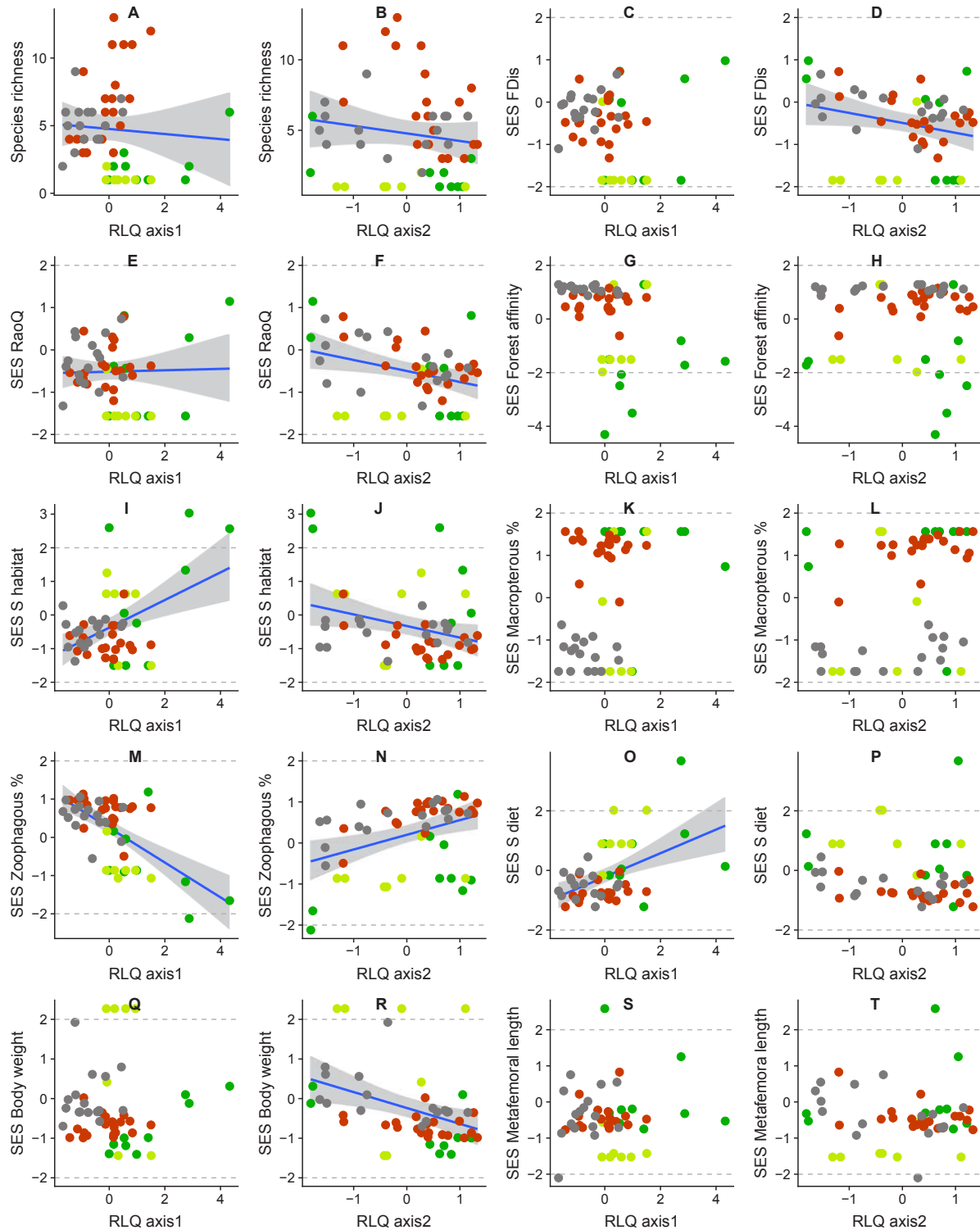


Figure S3.3 - Correlations between the community scores on the first two axes of the RLQ and their taxonomic and functional diversity: (A-B) observed species richness, (C-D) SES of functional dispersion, (E-F) SES of the RaoQ quadratic entropy, (G-H) SES of species affinity for forest ecosystems, (I-J) SES of the diversity of habitat used by species, (K-L) SES of the proportion of macropterous species; (M-N) SES of zoophagous behaviour, (O-P) SES of trophic niche breadth, (Q-R) SES of body weight, (S-T) SES of metafemoral length. Models are represented only for significant differences ($p < 0.05$). The horizontal dashed lines indicate standardized effect sizes of -2.0 and 2.0, which correspond to the approximate 5% significance level for individual SES values.

Chapter 3

The importance of saprophagous macroarthropods feeding behavior for their fecal pellets properties

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Abstract

Saprophagous macroarthropods are important actors of litter decomposition as they process large amount of litter and transform it into fecal pellets whose chemical and physical properties may depend on the litter species they consume. Despite their ability to feed on a wide range of food type, they exhibit feeding preferences based on litter palatability, but the role of feeding preferences for faeces properties as yet to be investigated. We compared the feeding preference and litter transformation capacity of six widespread macrodetritivore species feeding on a litter mix of four common tree species. We tested whether difference in diet composition due to feeding preferences would result in different faeces properties and how it could relate to the consumed litter identity and macrodetritivore identity and traits. Chemical and physical leaf traits (C:N:P ratio and tannins content) were important predictor for the consumption of one high-quality litter species but failed to explained the higher consumption of a low-quality species. Instead, the use of this nutritionally poor species leaves as microhabitat by arthropods may explain its higher consumption. Further, we show that faeces properties could be linked to the diet composition (litter identity effect), be of average quality independently of the consumer diet (macrodetritivore homogenization effect) but also depend on macrodetritivore specific digestion capacity. Finally, consumption and excretion rate as well as degree of food specialization was linked to species identity and body mass. Our results give further details on the mechanisms through which saprophagous macroarthropods affect litter decomposition in ecosystem where they are abundant. Using a large number of macrodetritivore species, we show that morphological traits as well as phylogenetic affiliation can partly explain feeding behavior and the outcome of litter transformation into faecal pellets.

Keywords

feeding preferences, litter transformation, palatability, microhabitat, consumption rate, faeces production

4.1. Introduction

A huge diversity of heterotrophic soil organisms organized in complex food webs participate in the decomposition of dead organic matter of mainly plant origin (Bardgett and Wardle 2010). The enzymatic breakdown of organic molecules during decomposition is mostly driven by microorganisms (Cadisch and Giller 1997; Berg and McClaugherty 2014), but soil fauna that modify plant litter quality and interact with microbial communities, play a critical role throughout the decomposition process as well (David 2014b; Joly et al. 2018). For example, saprophagous arthropods (e.g. millipedes, insect larvae, or woodlice) are important actor of litter decomposition where they are abundant as they can consume up to 50% of the total annual litter input (David and Gillon 2002). As these animals typically have low assimilation rates, they produce large amounts of faecal pellets composed of poorly digested material (Wolters 2000), which continues in the decomposition process. Litter conversion into faecal pellets is associated with a number of chemical and physical transformations of organic matter that alters considerably the further decomposition compared to the initial litter material (Joly et al. 2018). Chemical transformations following litter conversion into faecal pellets are the result of digestion through the activity of the enzymes produced by the animal itself or by its associated microbiota (Swift et al. 1979; Zimmer 2002). It typically leads to lower C:N and C:P ratios as well as condensed tannins in the faeces compared to the initial leaf litter material (Gunnarsson and Tunlid 1986; Kautz et al. 2002; Coulis et al. 2009; Bastow 2011; Joly et al. 2018). Physical transformations are mostly the result of litter fragmentation into smaller pieces (litter comminution) of 2 to 40 μm (Hartenstein 1964) that are assembled in faecal pellets of different size, shape, and compactness depending on the detritivore species (David 2014b).

Because the quality of organic matter is a major determinant of decomposition, evaluating changes in the quality following litter conversion into faecal pellets are key to assess the impact of litter processing by detritivores on the fate of organic matter. Previous studies demonstrated that conversion into faeces may homogenize initial litter differences, resulting in less variable microbial abundance and activity in the faeces than in the ingested litter (Suzuki et al. 2013; Joly et al. 2018). This homogenization capacity implies that detritivores are able to induce different quality change depending on the litter type they ingest, with

enrichment of low-quality litter (notably tannins hydrolysis) and impoverishment of high-quality litter (notably simple sugar absorption). However, such homogenization may be litter species-specific and faeces properties remain to a certain extent controlled by the initial litter properties (Joly et al. 2015), especially when litter type strongly differ (Wickings et al. 2012). Therefore, faeces properties depend on what the animal actually ingest from the available food in natural systems that usually is more diversified than in experimental studies. Assessing detritivore-driven changes in organic matter quality therefore requires tackling concomitantly feeding choice of animals and quality changes associated with each particular litter type.

Despite the capacity of detritivores to feed on a wide variety of resources and their general omnivory (Zimmer 2002), they exhibit feeding preferences that can be explained by different characteristics of their food determining litter palatability to saprophagous arthropods. Overall, macro-detritivore prefer high nutrient content (low C:N and C/P ratio), low deterrent compounds content like tannins, as well as low thickness (that correlates with litter toughness) or lignin concentration, which are all affected by the decay stage of litter (Zimmer 2002; David and Handa 2010; Gerlach et al. 2012; Wood et al. 2012; Quadros et al. 2014). These characteristics together determine litter palatability to saprophagous arthropods that consequently choose selectively their food items depending on these characteristics (Zimmer 2002). At the same time, the morphology of individual leaves, such as curliness, and the structure of the litter layer (Makkonen et al. 2012; Grootemaat et al. 2017) determine available microhabitats and their complexity and influence soil arthropod communities living in a “house made of food” (Hansen and Coleman 1998; Dias et al. 2017; Fujii et al. 2020). The use of a leaf as a microhabitat may promote its decomposition through its direct consumption by saprophagous arthropods or higher microbial activity by the deposition of arthropods faeces on the leaf surface (Frouz and Šimek, 2009, but see Coulis et al., 2013).

Most studies on macrodetritivore transformation of organic matter and feeding preferences are limited to a rather restricted number of animal species, with generally one (Bastow 2011; Joly et al. 2018; Coq et al. 2020), occasionally up to three (Zimmer et al. 2002b; Coq et al. 2018), and rarely four (Quadros et al. 2014) and five species (Ardestani et al. 2019). Although experimentally challenging, including multiple species in such studies is necessary to capture species-specific feeding behavior and capacity to transform organic matter (Zimmer and Topp

2000; Zimmer et al. 2002b). A species diet composition depend on its nutritional needs, its ability to assimilate nutrient and digest deterrent molecules, and is the result of interspecific resource and habitat partitioning (Zimmer and Topp 2000). It is also possible to link a species feeding behavior and its consumption and assimilation (and production of faeces as a consequence) to their body size. Metabolic scaling theory predicts that metabolic rate (tightly linked to consumption and faeces production rate) should scale with body mass with an exponent of $\frac{3}{4}$ (Brown et al. 2004b). Soil and litter animal follow the same relationship (Frears et al. 1996; Meehan 2006) and larger species exhibit lower mass-specific consumption rate (Biwer 1961; Coq et al. 2018; Ardestani et al. 2019). Although not tested specifically on soil invertebrates, direct positive link between body size and diet diversity have been reported in herbivores insects (Lepidoptera, Orthoptera), and is explained by larger mouthparts able to process wider type of food, and better digestive capacity (Bernays 1998).

Feeding preferences and transformation of leaf litter in faecal pellets are therefore both important to explain the role of detritivores in plant organic matter decomposition. To our knowledge however, these two mechanisms have not been studied at the same time. Here, we propose to experimentally assess the feeding behavior of six different macroarthropod species (three isopods and three millipedes) feeding on a mix of four litter species with contrasting chemical and physical characteristics and describe changes in these characteristics upon transformation into faeces. We hypothesized that (H1) feeding preferences will depend on the litter physico-chemical quality, e.g. higher consumption of litter species with higher nutrient content. Regarding litter transformation, faeces properties will depend on saprophagous macroarthropods diet composition, nutritional requirement, and ability to digest complex molecules (e.g. tannins, lignin). We therefore made the hypothesis that (H2) litter transformation and homogenization capacity, and therefore faeces properties will be macrodetritivore species-specific.

4.2. Material and methods

4.2.1. Leaf litter and animal collection

We selected six macrodetritivore species that often co-occur and are widespread in Western Europe, including the woodlice (Isopoda: Oniscidae) *Armadillidium vulgare* Latreille 1804

(Armadillidae), *Armadillo officinalis* Duaméril 1816 (Armadillidae), *Porcellio laevis* Latreille 1804 (Porcellionidae), and the millipedes (Myriapoda: Diplopoda) *Glomeris marginata* Villiers 1978 (Glomeridae), *Cylindroiulus caerulocinctus* Wood 1864 (Julidae), and *Ommatoiulus sabulosus* L. 1758 (Julidae). Individuals were collected by litter hand sorting in different Mediterranean forests surrounding the city of Montpellier in Southern France (Table S3.1). Animals were kept in large plastic boxes with leaf litter from the sites they were collected in and placed in climatic chambers. Leaf litter from four common Mediterranean tree species were selected: *Acer monspessulanum* L. 1753 (Sapindaceae), *Arbustus unedo* L. 1753 (Ericaceae), *Quercus ilex* L. 1753 (Fagaceae), *Quercus pubescens* Willd. 1796 (Fagaceae). These species are widespread in the Mediterranean basin of south of France, often found in mixed forests, and strongly differ in their leaf chemical, physical and morphological traits, leaf lifespan, and litterfall phenology. Leaf litter was collected in different forests located nearby Montpellier (Table S4.1) with suspended litter traps for *A. monspessulanum* and both *Quercus* species, and from the ground for *A. unedo*, since for this species, field work was done a little bit after peak leaf litter fall. However, the freshly fallen leaves were clearly distinguishable on the forest floor and we selectively collected only these recently fallen leaves. This and the fact of the dry weather makes it reasonable to assume that decomposition did not yet start. Litter material was dried at 30°C for 48 hours.

4.2.2. Leaf litter chemical and physical properties

Five subsamples per litter species were ground to a uniform particle size of 1 mm (Cyclotec Sample Mill, Tecator, Höganäs, Sweden). Total carbon (C) and nitrogen (N) concentrations were measured with a flash CHN Elemental Analyzer (Flash EA1112 Series, ThermoFinnigan, Milan, Italy). Phosphorus (P) concentration was measured colorimetrically after a mineralization step (Fanin et al, 2011) with an autoanalyzer (SmartChem 200, Alliance Instruments, Roma, Italy). Tannin concentrations were measured with the protein-precipitable phenolics microplate assay, a microplate protocol adapted from Hagerman and Butler (Hagerman and Butler 1978), following Hagerman 2011. Litter water holding capacity (WHC) was estimated by weighing six individual dried leaves per species and then re-watering them according to the protocol mentioned above, i.e. by immersing the leaves during one minute in deionized water. The leaves were then kept in closed boxes used as microcosms in

our study and re-weighed after 24h after removing excess water. Immediately after WHC measurement, leaf thickness was measured on 8 points per leaf avoiding leaf veins with a caliper to the nearest μm (Digimatic micrometer, Mitutoyo 0-25mm). Litter curliness was measured on 20 leaves per litter species according to Grootemaat et al (2017) i.e. by measuring the height of a leaf when it is deposited on a flat surface. On the same leaves, we developed a measure of litter tubularity by calculating the ratio of dry leaf projected surface area (A_{folded}) over its total surface area (A_{total}) when flattened in a scanner in moist conditions. Tubularity was then calculated with the formula

$$Tubularity = 1 - \frac{A_{\text{folded}}}{A_{\text{total}}} \quad \text{eq. 1}$$

Tubularity is comprised between 0 and 1, with increasing values for highly folded leaves. We then calculated Specific Leaf Area (SLA) as the ratio between leaf total surface area and dry mass. Litter 3-dimensionality (Makkonen et al, 2012) was estimated by measuring the volume occupied in an Erlenmeyer flask with three different batches of leaves of known dry mass for each species. The size of glass flasks varied depending on the leaf size for accurate measurements and we used mean species SLA value to convert the mass of litter per unit of volume into surface of litter per unit of volume. Leaf litter curliness and 3-dimensionality are important determinants for litter layer volume and heterogeneity, while tubularity is relevant for leaf-level microhabitat structure. All litter characteristics of each litter species are summarized in Table 4.1.

4.2.3. Microcosms and experimental conditions

One day before the start of the experiment, we moistened one gram ($1.04 \pm 0.03\text{g}$) of each litter type by dumping it in deionized water during one minute before removing adhering water drops. Fifty individuals of each detritivore species were selected, taking care not to include gravid females and to have a representative sample of species body size range. The individuals were distributed in plastic boxes with a moistened tissue for 24 hours until their guts were empty. Litter of the four species ($4.16 \pm 0.06\text{ g}$) were mixed and placed with 10 animals per species in $115 \times 85 \times 43\text{ mm}$ transparent plastic boxes (Caubert, Yèbles, France, Reference LAB3), yielding a total of five boxes per animal species. An additional 15 microcosms without fauna were set up as controls. We used five climatic chambers (LMS, Sevenoaks,

England) as the unit of replication, with one box of each animal species treatment and three boxes without animals in each climate chamber (i.e. nine boxes in each climate chamber). Every three days the microcosm (boxes) positions within each climatic chamber were randomized and litter moisture was maintained constant by adding 0.8 mL of deionized water to all microcosms. The experiment lasted 15 days with a day/night duration of 12/12 h and a temperature of 17/12 °C.

Table 4.1 – Differences in leaf litter properties between the four tree species. Microbial D= mass loss due to microbial activity only (from control microcosms, n=15), WHC= Water Holding Capacity. Small case letter indicate significant differences between species after Tukey post-hoc test on the one-way A

Trait	Litter species			
	<i>A. monspessulanum</i>	<i>A. unedo</i>	<i>Q. ilex</i>	<i>Q. pubescens</i>
Proportion of detritivore' diet (%)	30.5 ± 15.7 ^{ab}	41.2 ± 10.6 ^a	19.9 ± 4.3 ^{bc}	8.4 ± 6.1 ^c
C:N ratio	74 ± 1.8 ^a	189.3 ± 3.5 ^b	72.9 ± 3.4 ^a	45.8 ± 0.9 ^c
C:P ratio	216.3 ± 14.1 ^a	4360.8 ± 349.2 ^b	6715.2 ± 803.4 ^c	487.6 ± 46.4 ^a
N:P ratio	2.9 ± 0.2 ^a	23.1 ± 2.1 ^b	92.2 ± 10.6 ^c	10.7 ± 1.1 ^a
Microbial decomposition (%)	0.08 ± 0.02 ^a	0.01 ± 0.03 ^b	0.04 ± 0.03 ^{bc}	0.06 ± 0.05 ^{ac}
Tannins (%)	1.4 ± 0.3 ^a	4.3 ± 1.1 ^b	1.0 ± 0.1 ^a	0.9 ± 0.2 ^a
WHC (%)	144.9 ± 23.6 ^a	67.4 ± 6.1 ^c	90.6 ± 20.5 ^{bc}	122.2 ± 30.7 ^{ab}
Thickness (µm)	173.3 ± 15.3 ^a	317.4 ± 48.2 ^b	370.3 ± 37.2 ^c	232.5 ± 40.5 ^d
SLA (g.mm ⁻²)	112.5 ± 23.9 ^a	70.2 ± 23.7 ^b	55.6 ± 11.6 ^b	108.8 ± 23.1 ^a
Curliness (mm)	14.4 ± 4.3 ^a	7.9 ± 2.1 ^b	7.3 ± 3.7 ^b	14.7 ± 5.6 ^a
Tubularity	0.2 ± 0.1 ^a	0.5 ± 0.1 ^b	0.1 ± 0.1 ^c	0.1 ± 0.1 ^c
3-Dimensionality (mm ² .cm ⁻³)	6.2 ± 0.3 ^a	27.6 ± 1.4 ^b	28.4 ± 0.9 ^b	6.3 ± 0.4 ^a

Table 4.2 – Macrodetritivore physiological traits. MSA= mass specific area, sp= specific. Small case letter indicate significant differences between species after Tukey post-hoc test

	Detritivore species					
	<i>A. officinalis</i>	<i>A. vulgare</i>	<i>P. laevis</i>	<i>G. marginata</i>	<i>C. caerulocinctus</i>	<i>O. sabulosus</i>
Biomass ¹	0.19 ± 0.01 ^a	0.12 ± 0.02 ^b	0.09 ± 0.01 ^b	0.16 ± 0.01 ^a	0.08 ± 0.02 ^b	0.24 ± 0.04 ^c
Individual consumption ²	1.15 ± 0.57 ^a	2.26 ± 1.29 ^a	1.22 ± 0.39 ^a	1.28 ± 0.27 ^a	1.06 ± 0.43 ^a	1.91 ± 0.25 ^a
Mass sp consumption ³	6.07 ± 2.78 ^a	18.87 ± 9.63 ^b	13.85 ± 4.33 ^{ab}	7.81 ± 1.69 ^a	12.22 ± 3.89 ^{ab}	8.01 ± 1.85 ^a
Diet diversity ⁴	1.19 ± 0.03 ^a	1.10 ± 0.14 ^a	0.99 ± 0.23 ^a	1.24 ± 0.14 ^a	0.98 ± 0.29 ^a	1.22 ± 0.15 ^a
Individual faeces production ²	0.83 ± 0.37 ^{ab}	1.83 ± 1.12 ^a	0.81 ± 0.17 ^b	1.06 ± 0.27 ^{ab}	0.94 ± 0.29 ^{ab}	1.35 ± 0.20 ^{ab}
Mass sp faeces production ³	4.37 ± 1.79 ^a	15.22 ± 8.43 ^b	9.11 ± 1.24 ^{ab}	6.40 ± 1.28 ^a	10.95 ± 1.99 ^{ab}	5.60 ± 1.12 ^a
Assimilation ⁵	26.2 ± 7.8 ^a	19.1 ± 15.3 ^a	32.1 ± 19.4 ^a	16.7 ± 11.6 ^a	10.9 ± 10.5 ^a	28.3 ± 14.3 ^a
Faeces MSA ⁶	5.59 ± 0.73 ^a	4.11 ± 0.74 ^{ab}	4.19 ± 0.50 ^{ab}	3.0 ± 0.32 ^b	3.37 ± 1.08 ^b	2.58 ± 0.64 ^b

¹ grams ; ² mg.ind⁻¹.day⁻¹ ; ³ mg.g⁻¹.fresh weight⁻¹.day⁻¹ ; ⁴ Shannon index ; ⁵ % ; ⁶ mg.mm⁻²

4.2.4. Detritivore feeding behavior and diet and faeces properties

At the end of the experiment, faecal pellets and remaining litter of each species were sorted and placed in the oven at 30 °C for 48 h and then weighed to the nearest 0.01 mg. Animals were sorted out, kept without food for 24 h to empty their guts and then weighed before being released. The final animal fresh mass was used for later calculations. To quantify animal consumption of each litter species we used the formula given by David (1998).

$$C = \frac{M_0 - M_0 D - M_f}{\sqrt{1-D}} \quad \text{eq. 2}$$

with M_0 = initial litter dry mass, M_f = final litter dry mass. D is the contribution of microbial-driven decomposition to each litter species mass loss, i.e. the mean proportion of litter decomposed in the absence of macrodetritivores for each species and was calculated as $D = (M'_0 - M'_f)/M'_0$, with M'_0 and M'_f the initial and final litter dry mass in control boxes, respectively. The calculated consumption C was then reported to the duration of the experiment (15 days) and to the number of individuals (10) to obtain individual consumption rate ($\text{g.ind}^{-1}.\text{day}^{-1}$) and to the final fresh mass of fauna to obtain mass-specific consumption rate ($\text{g.g}_{\text{fresh weight}}^{-1}.\text{day}^{-1}$) as in David and Gillon (2002). Consumption values were calculated for each litter species separately and summed up to obtain total consumption by detritivore. Individual and mass-specific faecal pellet production rates were calculated by dividing total faeces mass by the experiment duration and the number of individuals of detritivores or their total fresh weight, respectively. Assimilation rates were estimated by calculating the difference between mass-specific consumption and faeces production rate. To quantify detritivore diet diversity, we calculated the Shannon diversity (Shannon 1948) of the detritivore mass-specific feeding rate of each litter species. Independently of consumption rate, this index informs on the diversity of the elements constituting the animals' diet. To estimate the quality of the available litter and ingested litter (diet), we calculated the community weighted mean trait using the following formula:

$$CWM(X)_m = \sum_{i=1}^4 c_i * trait_i \quad \text{eq. 3}$$

Where c_i is the relative proportion of litter available in the mixture, or detritivore mass-specific consumption of litter species ($\text{g.g}_{\text{fresh weight}}^{-1}$) and $trait_i$ is the mean value of trait X of litter species i . Faeces C, N, P, and tannin content were measured following the same protocol as

for leaf litter. Faeces WHC capacity was measured according to Joly et al, (2018). Faeces specific area ($\text{mm}^2.\text{mg}^{-2}$) was measured by calculating the projected surface area of 10 faecal pellets from photographs using a stereo-microscope and reporting it to their total dry mass.

4.2.5. Statistical analysis

Differences between macrodetritivore species characteristics (diet diversity, consumption rate, assimilation rate, and faeces production rate), faeces traits as well as differences between litter species physico-chemical and morphological properties were tested using one-way ANOVA (using *lm* function from *stats* package R) followed by post-hoc Tukey test (*HSD.test* function, package *agricolae*) on the R software v.3.5.2 (R Core Team 2019). The six animal species differed in their mean fresh weight ($F_{5,24} = 54$, $pval < 0.001$; Table 4.2). Therefore, the effect of detritivore identity and fresh weight were tested separately. Differences between available diet and faeces quality and available litter quality were separately tested by one-way ANOVA. The relationship between faeces and food properties was tested by linear regression with the properties that were measurable on both material i.e. C:N, C:P, and N:P ratios, tannins content and WHC. Further, we tested the importance of macrodetritivore physiological traits and feeding behavior for faeces properties by modelling faeces C:N, C:P, and N:P ratios, tannins content and WHC with mass specific consumption and faeces production rate, assimilation rate, and diet diversity. The best model was selected with the *dredge* function (*MuMIn* package) by keeping the best models within a ΔAIC of 2, and rejecting all models if the null model was included (Harrison et al. 2018b). To assess which litter properties influenced animal feeding preferences, we constructed individual regression models between each litter species relative consumption by each detritivore species (in relation to the total amount of litter consumed) and the different litter properties (Quadros et al. 2014). This approach was used because the limited number of litter species and the high collinearity between litter properties (Fig. S4.1) made impossible to include all litter properties as independent variable in the same model.

4.3. Results

4.3.1. Litter properties

Litter species strongly differed in their chemical, physical and morphological traits (Table 4.1). *A. monspessulanum* had the lowest C:P and N:P ratio and leaf and highest WHC and SLA. It also showed high curliness value and three-dimensionality but low tubularity. *A. unedo* was of poor nutritional quality with the highest C:N ratio and tannins content and lowest WHC, but had the highest tubularity value due to its cylindrical shape. *Q. ilex* was N-rich but P-poor with low tannins concentration and was the thickest litter species. It was the only species with low values of curliness, tubularity, and 3-dimensionality. Finally, *Q. pubescens* had the lowest C:N ratio and tannins content, intermediate value of P, and physical traits, and the same morphological characteristics as *A. monspessulanum*.

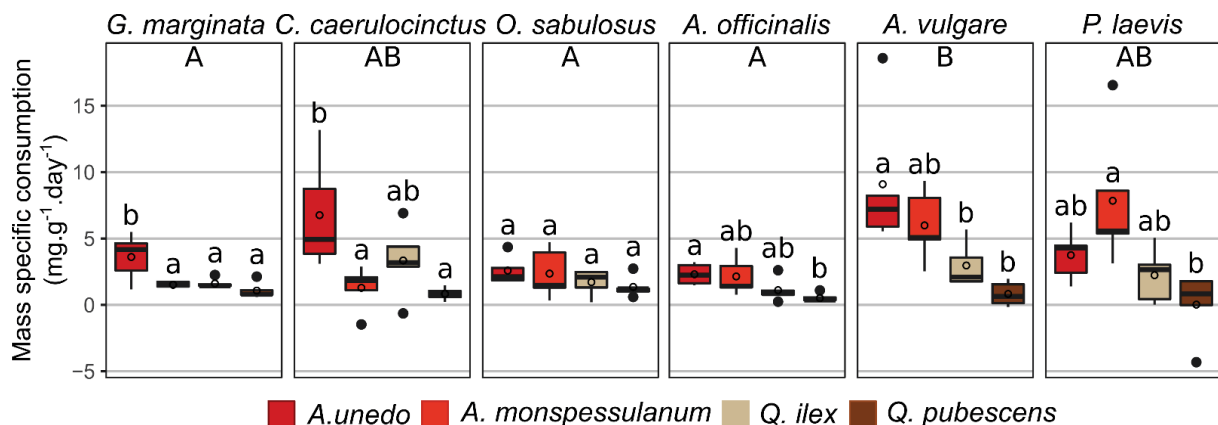


Figure 4.1 – Mass specific consumption rate ($\text{g.g}^{-1}_{\text{faune}}.\text{day}^{-1}$) of each macrodetritivore species. Differences between species mean value across all litter species are shown by uppercase letter, and differences between litter species mean value for each macrodetritivore species are shown with lowercase letter. Difference were tested by post-hoc Tukey test ($\alpha=0.05$).

4.3.2. Detritivore feeding preferences

All saprophagous macroarthropod species fed on all litter species (except *P. laevis* that on average did not feed on *Q. pubescens*). Across all animal species *A. unedo* litter was consumed the most, with on average 42 % of the diet, followed by *A. monspessulanum* (32 %), *Q. ilex* (9%), and *Q. pubescens* (7 %). However, none of the six detritivore species had exactly the same diet (Fig. 3.1, Fig. S3.2). In line with the overall average, the two millipede species *G.*

marginata and *C. caerulocinctus* showed the highest consumption rates on *A. unedo* litter. In contrast, the isopod *P. laevis* consumed *A. monspessulanum* at the highest rate (though not significantly different from *A. unedo* and *Q. ilex*), and isopods in general consumed *A. monspessulanum* litter at comparatively high rates similar to *A. unedo*. *O. sabulosus* was the only species without significant feeding preferences. Among the ten litter properties, C:N ratio, tannins content, and tubularity significantly correlated with litter preferences by detritivores, while none of the physical properties affect feeding preferences (Table 4.3, Fig. S4.3). Saprophagous macroarthropods therefore preferred leaves with higher C:N ratio, tannins content, and tubularity index, corresponding to *A. unedo* properties.

	<i>Df</i>	<i>SS</i>	<i>F</i>	<i>pval</i>
CN	1	2953.4	19.9	<0.001
CP	1	5455.7	0.7	0.410
NP	1	5551.8	0.3	0.581
T	1	3115.4	17.8	<0.001
Thickness	1	5599.6	0.1	0.729
SLA	1	5353.8	1.1	0.298
WHC	1	5014.4	2.7	0.114
Tubularity	1	3132.9	17.5	<0.001
Curliness	1	4944.7	3.1	0.095
3-dimensionality	1	4949.5	3.0	0.096

Table 4.3 - ANOVA table of linear regression between litter preference by saprophagous macroarthropods (proportion of the litter type in the animal diet) and each litter properties

4.3.3. Detritivore physiological traits and feeding behavior

Total consumption rates across all litter species were highest in *A. vulgare* (Table 4.2, Fig. 4.2), intermediate in *P. laevis* and *C. caerulocinctus* (although not significantly different from all other species, Table 4.2), and lowest in *A. officinalis*, *G. marginata*, and *O. sabulosus*. No difference between species was observed regarding individual consumption rate (Table 4.2, Fig. S4.4). The rate of faeces production (individual and mass-specific) mirrored largely consumption rates with *A. vulgare* producing more than three times more faeces than *A. officinalis* that had the lowest faeces production rate (Table 4.2). Individual consumption and faeces production rates did not relate to animal fresh weight, while mass-specific rates were negatively correlated to body mass (Fig. 4.2, Table S4.2). The diet diversity (Shannon) did not differ between species but increased with species body mass, while not being significantly related to mass specific consumption rate (Fig. 4.2, Table S4.2). Assimilation rate was not different between species and was not influenced by animal fresh weight.

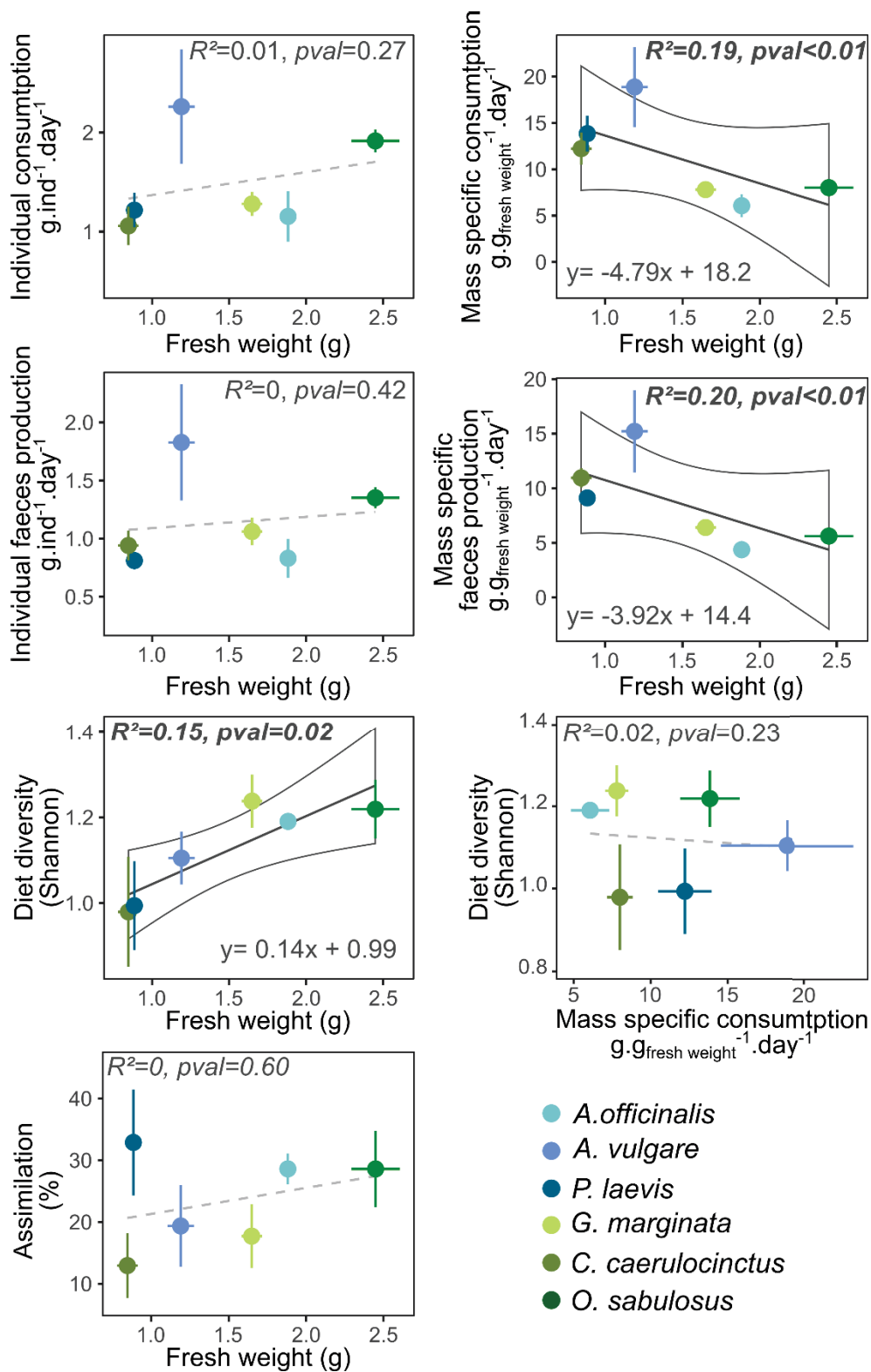


Figure 4.2 – Macrodetrivore physiological trait relationships to species fresh body mass (g). The grey line is the linear regression with 95% confidence interval when significant, dashed otherwise. Adjusted R^2 , p -value, and the linear regression equation of significant relationships are shown.

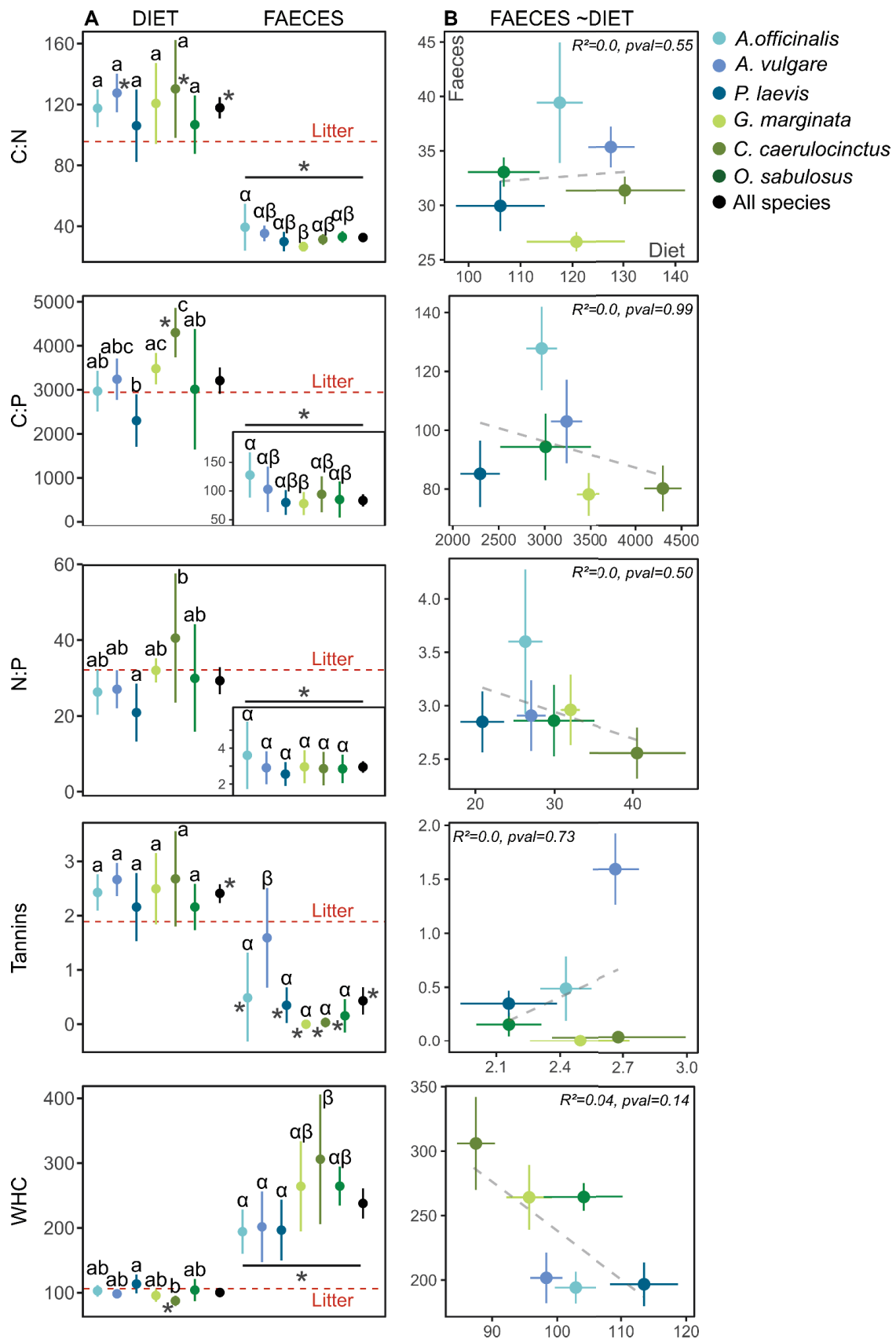


Figure 4.3 – Changes in C:N, C:P, N:P ratio, Tannins content (%), and Water Holding Capacity (WHC) between **A** available litter (dashed orange line) and ingested food and faeces respectively and **B** between ingested food and faeces. Dashed grey line (panel B) is the linear regression, no confidence interval is shown as none of the regression was significant. Smallcase and greek letter indicate significant differences after Tukey post-hoc test on the detritivore species identity effect on food and faeces trait respectively. Adjusted R^2 and p-value are displayed.

4.3.4. Links between litter, diet, and faeces traits

When all detritivore species were pooled, diet properties differed significantly from the available litter properties across with higher C:N ratios and tannins content (Fig. 4.3). These differences were maintained for two individual species with higher C:N and C:P ratio and lower WHC in *C. caerulocinctus* diet and higher C:N ratio in *A. vulgare* diet (Fig. 4.3A). All species faeces had lower C:N, C:P, and N:P ratio and tannins content and higher WHC than initial litter, except for *A. vulgare* faeces tannins content that did not differ from that of the litter. Faeces traits were not related to food traits (Fig. 3B) but differed between species (Fig. 4.3A, Table S4.3). *G. marginata* faeces had the lowest value of C:N and C:P ratios and tannins content while *A. officinalis* faeces had the highest C:N and C:P ratio value and *A. vulgare* faeces had the highest tannins content. *C. caerulocinctus* produced faeces with the highest WHC value while *A. officinalis* produced low-WHC faeces. Detritivore faeces differed in their mass-specific area with the highest MSA faeces produced by *A. officinalis*, while the three millipede species produced faeces with low MSA (Table 4.2). Among C:N, C:P, N:P ratios, tannins content, and WHC, only faeces tannins content was related to macrodetritivore physiological traits. More precisely faeces tannins content increased both with consumption and faeces production rate (Table S4.4). Assimilation or diet diversity did not influence any of the faeces properties.

4.4. Discussion

4.4.1. Feeding preferences explained by leaf palatability and microhabitat properties

The six saprophagous macroarthropod included in our study showed clear preferences between the four litter species, and the pattern was detritivore species-specific. The most consumed litter species was *A. unedo* despite having the lowest palatability (low nutrient content, WHC, and microbial decomposition, and high tannins content and thickness), rejecting our first hypothesis. A first explanation would be that *A. unedo* tubular-shaped leaves maintained better microclimatic conditions such as higher moisture and lower light exposure, although actual measurement of such microclimatic conditions at the leaf scale are required. Microclimatic conditions are important for macroarthropods communities (Mueller et al. 2016) that likely consumed the litter they inhabited according to the “house made of food” concept (Anderson 1977; Fujii et al. 2020). Our study does not allow to disentangle nutritional

and microhabitat properties of leaves, and experimentally manipulate leaves morphology (e.g. cutting *A. unedo* in small pieces and rolling the other species leaves) would help dissociate food and habitat requirement effect on macroarthropods feeding behavior. However, the fact that the litter species with the lowest physico-chemical quality was the most consumed is a strong indicator that other litter characteristics than strict physico-chemical quality are important in determining macroarthropod feeding preferences. Secondly, the better microclimatic conditions along with deposition on the leaf surface of fresh faeces with transiently enriched bacteria communities likely promoted microbial colonization of the litter, which is known to increase litter palatability to macrodetritivore (Maraun and Scheu 1996; Zimmer et al. 2003; Harrop-Archibald et al. 2016). Finally the consumption of *A. unedo* may have been facilitated by the parallel consumption of *A. monspessulanum* as it was the second highest consumed litter species (32% of animals' diet on average, from 11 to 57% of *C. caerulocinctus* and *P. laevis* diet respectively). This species litter was of high physico-chemical quality and showed the highest microbial decomposition rate. The mixed diet of all macrodetritivore species likely permitted them to reach their nutritional demands, allowing them to feed of poor-quality litter. The fact that species feeding preferences were only linked to three litter characteristics is interesting as it could be used to predict animals' diet from a restricted number of traits. Our results further suggest that using litter morphological traits linked to microhabitat structure is promising to better explain macrodetritivore behavior and distribution in natural ecosystems (Fujii et al. 2020).

4.4.2. Feeding behavior and diet diversity are linked to detritivore species identity and body mass

Based on physiological and morphological traits, *A. vulgare*, *P. laevis*, and *C. caerulocinctus* formed a distinct group of smaller bodied taxa with high mass-specific consumption and faeces production rate and low diet diversity (Table 4.2, Fig. S4.5, Table S4.5). The negative relationship between body mass and mass-specific consumption and excretion rate is in line with the *metabolic theory* (Brown et al. 2004b; Meehan 2006) and several studies done on the same or closely related species, namely *G. marginata*, *C. caerulocinctus*, and *Ommatoiulus rutilans* (C. L. Koch, 1847) feeding on grass litter (Coq et al. 2018, 2020) and *G. marginata*, *G. hexasticha*, *C. caerulocinctus*, and *Porcellio scaber* feeding on *Alnus glutinosa* litter (Ardestani

et al. 2019). Interestingly, diet diversity differed between the six species and was positively related to organism body mass. Higher food specialization of smaller taxa have been reported for herbivorous insects (Lindström et al. 1994; Novotny and Basset 1999; Cizek 2005; Davis et al. 2013) but are less studied for soil invertebrates. Larger organisms may have a more diverse diets because their higher mandibular gape and chewing strength offset the consumption limits set by leaf thickness and toughness (Bernays 1986; Hochuli 2001). If litter thickness partially explained feeding preferences (high consumption of *A. monspessulanum* that was the thinnest), additional measurement of litter toughness are required to support this hypothesis. It is quite important to notice how the six species of our study were well differentiated regarding their diet composition. Despite saprophagous macroarthropods ability to feed on wide range of food source, coexisting species usually differ in their diet, nutritional requirement and digestion capabilities (Zimmer and Topp 2000; Zimmer et al. 2002b). Lower nutritional niche overlap is crucial for species coexistence, limits species redundancy in litter decomposition (Zimmer et al. 2004a) and is one mechanism explaining the importance of macrodetritivore diversity and community composition for litter decomposition through complementarity effects (Heemsbergen 2004; Hedde et al. 2010; De Oliveira et al. 2010; Coulis et al. 2015b). This niche differentiation hypothesis is supported by the fact that the six studied species often co-occur, notably in Mediterranean landscape (David et al. 1999). It is important to note that the six species included in our study varied only slightly in their body mass (2.5 fold between smallest and largest species). Further studies including taxa of more contrasted body size, spanning several order of magnitude would be interesting to test the observed patterns between body size and diet diversity and draw more general conclusions on the importance of soil invertebrate body size for litter mass loss (Frouz 2018).

4.4.3. Consequences of macrodetritivore species feeding and digestive capabilities for faeces properties

Macrodetritivore species differed in their faeces properties (except for N:P ratio), but the differences could be linked to diet difference. Therefore, diet and faeces quality were not significantly linked across species, meaning that faeces characteristics are mostly unpredictable from litter and diet characteristics. On average, faeces were of higher chemical quality (lower C:nutrient ratio, and tannins content) than the litter, which can strongly

facilitate microbial activity and organic matter decomposition. Indeed, by switching organic matter C:N and C:P ratio from 95.6 ± 0.7 and 2942 ± 32 in the litter to 32.6 ± 6.9 and 95.6 ± 29 in faeces macrodetritivore may promote microbial activity that usually is limited on substrate with C:N and C:P ratios above 30 and 92 (Kaye and Hart 1997; Čapek et al. 2016; Joly et al. 2018). Additionally, preferential consumption of the lowest-quality litter result in higher mean quality of litter at the community level, and favor microbial activity in the remaining litter (Coulis et al. 2013a).

One surprising result is the high tannin content of *A. vulgare* faeces that was similar to litter tannin content. The two other isopod species also had high faeces tannins content, and isopod faeces were richer in tannins than millipede faeces. Woodlice and millipede digestive tracks both consist in a simple straight tube, but isopod digestive track is shorter due to their small body length compared to julid-form millipede. This may result in shorter food retention time in the digestive system and likely reduce the digestion of complex molecules (Demment & Van Soest, 1985; Yang & Joern, 1994). Actual measurement of retention time of litter particles in macrodetritivore digestive tubes are required to confirm this assumption. Additionally, the pill millipede *G. marginata* waives the rule as it has a body length (i.e. digestive tube length) comparable to isopods, but faeces with no detectable tannins content. Low if not undetectable tannins content in *G. marginata* have already been reported when feeding on three litter type of varying tannins content and decay stage (Coulis et al. 2009) and on seven tree species (Joly et al. 2015), while tannins could be detected from isopods faeces feeding on different litter type (Zimmer et al. 2002a, b). Species and phylum-specific microbiota composition and bacterial diversity in the digestive tube may explain these difference since microbial communities largely contribute to macrodetritivore digestion and assimilation of food (Dittmer et al. 2016) but complete description of microbial communities in these animals digestive tube are lacking (König and Varma 2006). Finally, highest tannins content in faeces was linked to mass-specific consumption rate (and therefore faeces production rate) but not to assimilation, and *A. vulgare* processed litter faster than other species. This likely resulted in leaving less time for tannins and protein to complex in the animal digestive track, making tannins more detectable by the method employed. If not complexed to proteins, tannins

would also be more impacting for microbial activity and faeces and litter decomposition (Hättenschwiler and Vitousek 2000).

In addition to chemical changes, physical differences in faeces were observed with higher WHC of millipede than woodlice faeces. This difference was notably due to the highest faeces WHC of *C. caerulocinctus* whilst its food, dominated by low WHC-leaves of *A. unedo* and *Q. ilex* particles, was of lower WHC compared to the litter mix. This means that faeces WHC is not linked to the physical properties of the particles that constitute it, but rather to faeces specific area. Millipede produce thicker and rounded faecal pellets compared to the thin, flat and squared woodlice faeces. These structural differences likely determine faeces physical properties such as WHC, and strongly influence carbon and nitrogen cycle (David 2014b; Joly et al. 2018).

4.5. Conclusion

Our study contribute to the on-going effort to quantify soil biodiversity contribution to ecosystem processes. If we show that the result of litter transformation into faecal pellets is litter and macrodetritivore species-specific, we were able to predict part of their feeding behavior with their morphological traits. If further confirmed by other studies, differences observable at the class level (Isopoda vs Diplopoda) are valuable as they could be more easily incorporated in C and N cycling models than species-specific effects (Fry et al. 2019). The concomitant consumption of low quality litter and production of faeces with high nutritional value imply a strong chemical and physical reorganization of litter layer in ecosystems where macrodetritivore are abundant with consequences for the remaining litter decomposition (Coq et al. 2020).

Supporting Information

Table S4.1 – Biological material sampling site information

	Site of collection	Coordinates	Method of collection
Tree species			
<i>Acer monspessulanum</i>	Mas d'Arnaud	4360'N, 359'E	Litter traps
<i>Arbustus unedo</i>	Montarnaud	4339'N, 340'E	Ground collection
<i>Quercus ilex</i>	Puechabon	4344'N, 335'E	Litter traps
<i>Quercus pubescens</i>	CEFE	4363'N, 386'E	Litter traps
Detritivore species			
<i>Armadillo officinalis</i>	ECOTRON	4368'N, 388'E	Hand sorting
<i>Armadillidum vulgare</i>	Montarnaud	4339'N, 340'E	Hand sorting
<i>Porcellio laevis</i>	CEFE	4344'N, 335'E	Hand sorting
<i>Glomeris marginata</i>	Montarnaud	4339'N, 340'E	Hand sorting
<i>Cylindroiulus caerulocinctus</i>	Montarnaud	4339'N, 340'E	Hand sorting
<i>Ommatoiulus sabulosus</i>	Marseille	4336'N, 342'E	Hand sorting

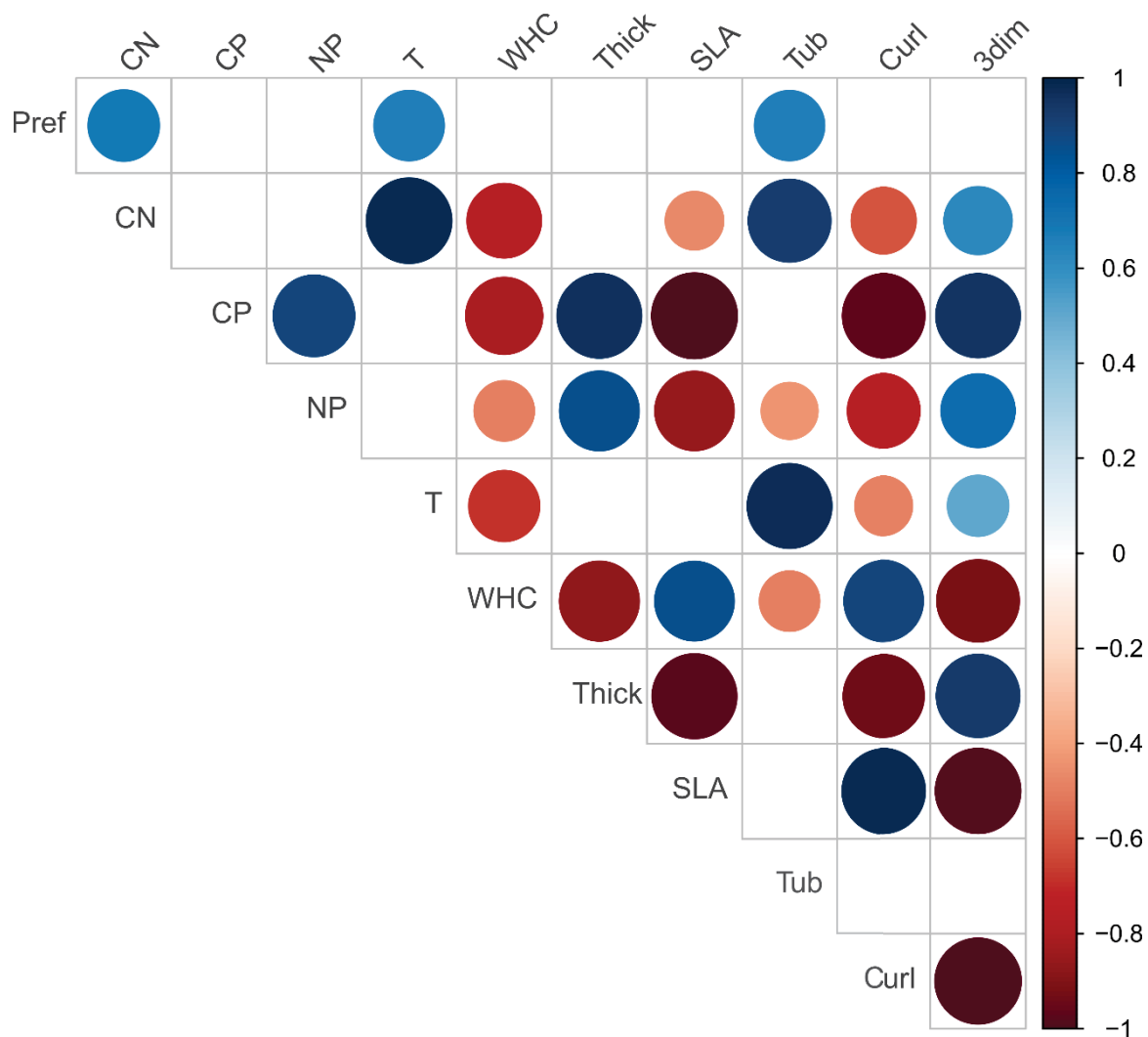


Figure S4.1 – Correlation (Pearson) plot between all leaf litter properties and litter preference by saprophagous macroarthropods. C:N:P: nutrient ratios, T: tannins content, Thick: thickness, WHC: water holding capacity, SLA: specific leaf area, Curl: curliness, Tub: tubularity, 3dim: 3-dimensionality. Circle color indicate the direction of the relationship (red: negative, blue: positive) and the circle size correspond to the strength of the relationship. Non significant correlations are represented by empty cells.

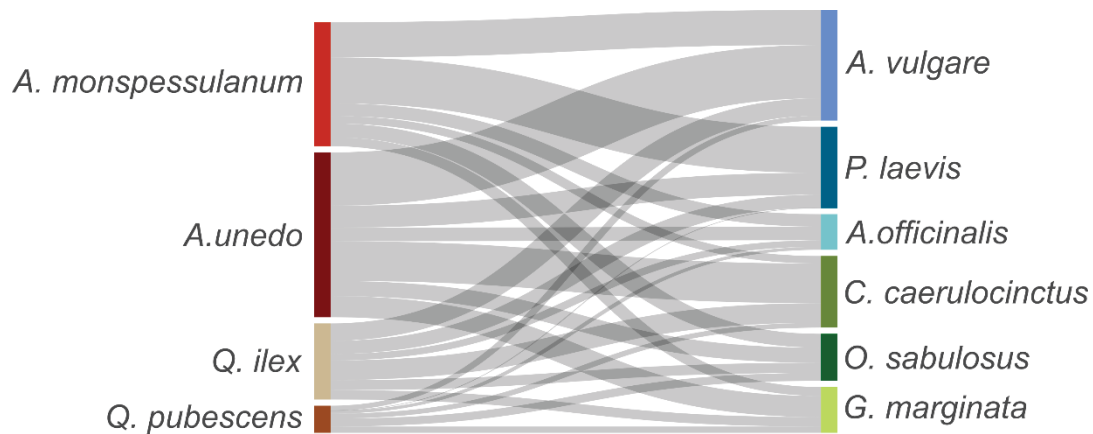


Figure S4.2 – Sankey diagram of the diet composition (proportion of each litter species) of the six saprophagous macroarthropods

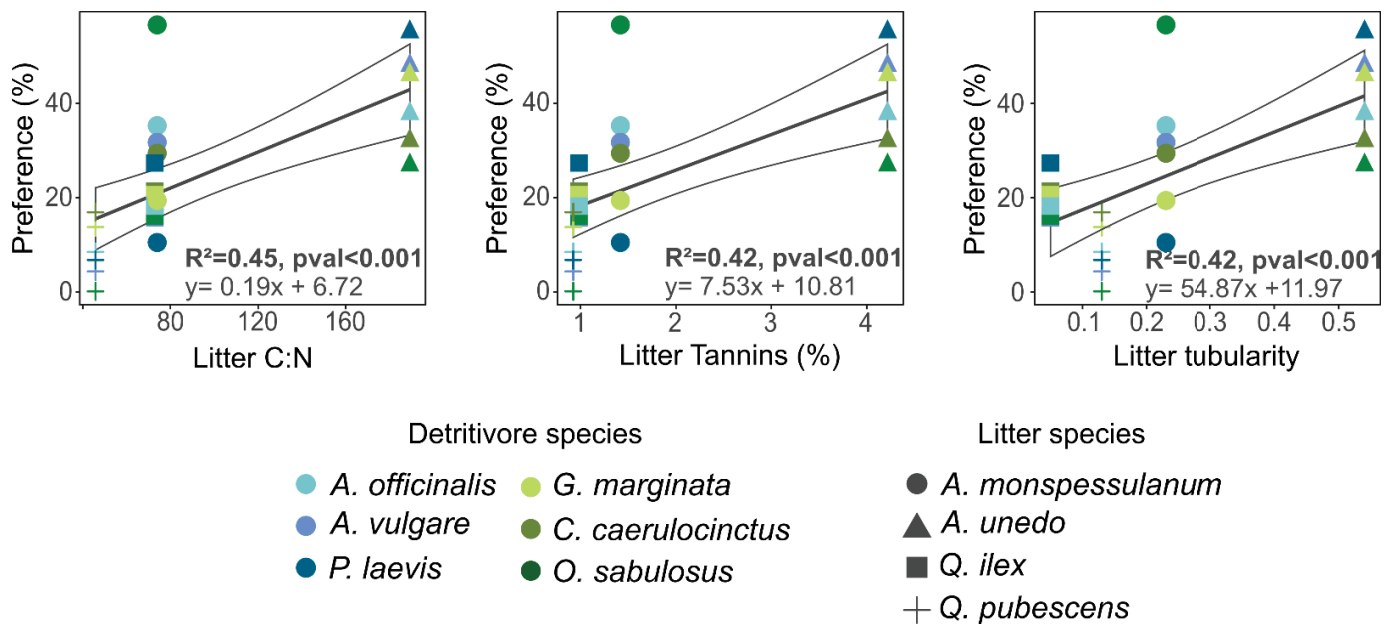


Figure S4.3 – Simple regression between litter CN, tannins content and tubularity and saprophagous macroarthropod preference for this litter (as proportion of the litter type in its diet).

Table S4.2 – Macrodetritivore physiological traits relationships to body mass and species identity

Response variable		Detritivore species					Body mass (g)					
		Df	SS	F	p	R ² adj	slope	Df	SS	F	p	R ² adj
Individual consumption ¹	Covariable	5	5.96	2.9	0.035 *	0.25	0.25 ± 0.22	1	0.68	1.2	0.27	0.01
	Residuals	24	9.89					28	15.18			
Mass specific consumption ²	Covariable	5	574.5	4.9	<0.01 **	0.40	-4.79 ± 1.72	1	246.5	7.8	<0.01 **	0.19
	Residuals	24	563.7					28	890.7			
Individual faeces production ¹	Covariable	5	3.83	2.9	0.036 *	0.24	0.15 ± 0.18	1	0.24	0.7	0.42	0.0
	Residuals	24	6.44					28	10.03			
Mass specific faeces production ²	Covariable	5	406.3	5.9	0.001 **	0.46	-3.92 ± 1.38	1	164.9	8.1	<0.01 **	0.20
	Residuals	24	330.2					28	571.6			
Assimilation ³	Covariable	5	1510.5	1.8	0.18	0.18	2.33 ± 4.38	1	58.1	0.3	0.60	0.0
	Residuals	24	4325.5					28	5777.9			
Diet diversity ⁴	Covariable	5	0.32	1.9	0.12	0.14	0.14 ± 0.06	1	0.20	6.0	0.02 *	0.15
	Residuals	24	0.8					28	0.92			

¹ mg.ind⁻¹.day⁻¹; ² mg.g_{fresh weight}⁻¹.day⁻¹; ³ %; ⁴ Shannon index

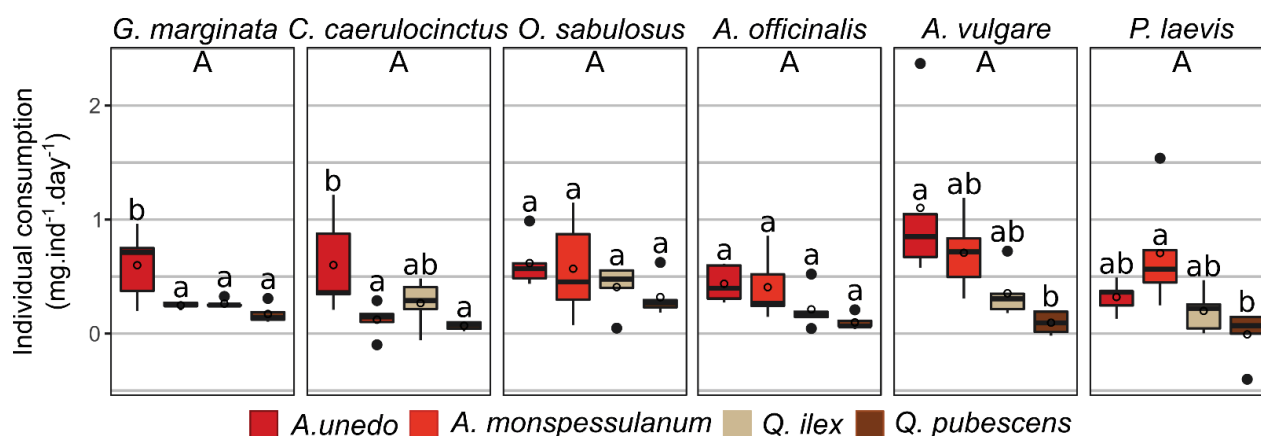


Figure S4.4 – Individual consumption rate (g.ind⁻¹.day⁻¹) by macrodetritivore species. Differences between species mean value across all litter species are shown by uppercase letter, and differences between litter species mean value for each macrodetritivore species are shown with lowercase letter. Difference were tested by post-hoc Tukey test.

Table S4.3 – Carbon, nitrogen, phosphorus, and tannins content, stoichiometric ratio, and water holding capacity (WHC) in litter, ingested litter (food) and faeces of each of the 6 detritivores species, and averaged per order (isopoda and diplopoda). Mean $\pm$ se are displayed with lowercase letter indicating significant differences after post-hoc Tukey comparison

	C %	C:N	C:P	N %	N:P	P %	T %	WHC %
Litter	48 $\pm$ 0	95.6 $\pm$ 0.7	2942 $\pm$ 32	0.65 $\pm$ 0	32.1 $\pm$ 0.4	0.09 $\pm$ 0	1.9 $\pm$ 0	106.3 $\pm$ 0.4
Food	48.2 $\pm$ 0.5	118.2 $\pm$ 18.9	3215 $\pm$ 809	0.52 $\pm$ 0.07	29.4 $\pm$ 9.7	0.09 $\pm$ 0.04	2.4 $\pm$ 0.5	100.3 $\pm$ 11.7
<i>Isopoda</i>	48 $\pm$ 0.5 ^a	117.1 $\pm$ 15.7 ^a	2834 $\pm$ 561 ^a	0.52 $\pm$ 0.05 ^a	24.7 $\pm$ 5.5 ^a	0.11 $\pm$ 0.03 ^a	2.4 $\pm$ 0.4 ^a	104.9 $\pm$ 10.3 ^a
<i>Diplopoda</i>	48.4 $\pm$ 0.5 ^b	119.3 $\pm$ 22.1 ^a	3595 $\pm$ 855 ^b	0.53 $\pm$ 0.09 ^a	34.1 $\pm$ 10.7 ^b	0.07 $\pm$ 0.04 ^b	2.4 $\pm$ 0.6 ^a	95.8 $\pm$ 11.5 ^b
<i>Armadillo officinalis</i>	48.1 $\pm$ 0.4 ^{ab}	117.5 $\pm$ 9.9 ^a	2967 $\pm$ 374 ^{ab}	0.52 $\pm$ 0.02 ^a	26.3 $\pm$ 4.8 ^{ab}	0.1 $\pm$ 0.03 ^{ab}	2.4 $\pm$ 0.3 ^a	102.9 $\pm$ 7.2 ^{ab}
<i>Armadillidium vulgare</i>	48.3 $\pm$ 0.2 ^{ab}	127.6 $\pm$ 10.3 ^a	3238 $\pm$ 379 ^{abc}	0.48 $\pm$ 0.05 ^a	27 $\pm$ 4.1 ^{ab}	0.09 $\pm$ 0.02 ^{ab}	2.7 $\pm$ 0.2 ^a	98.3 $\pm$ 5.5 ^{ab}
<i>Porcellio laevis</i>	47.6 $\pm$ 0.6 ^a	106.1 $\pm$ 19.1 ^a	2297 $\pm$ 479 ^b	0.55 $\pm$ 0.05 ^a	20.9 $\pm$ 6.1 ^a	0.14 $\pm$ 0.04 ^a	2.2 $\pm$ 0.5 ^a	113.5 $\pm$ 11.7 ^a
<i>Glomeris marginata</i>	48.4 $\pm$ 0.3 ^{ab}	120.7 $\pm$ 21.4 ^a	3478 $\pm$ 288 ^{ac}	0.53 $\pm$ 0.1 ^a	32 $\pm$ 2.6 ^{ab}	0.07 $\pm$ 0.01 ^b	2.5 $\pm$ 0.5 ^a	95.7 $\pm$ 7.8 ^{ab}
<i>Cylindroiulus caerulocinctus</i>	48.8 $\pm$ 0.4 ^b	130.3 $\pm$ 25.9 ^a	4297 $\pm$ 451 ^c	0.48 $\pm$ 0.09 ^a	40.5 $\pm$ 13.7 ^b	0.04 $\pm$ 0.01 ^b	2.7 $\pm$ 0.7 ^a	87.5 $\pm$ 6.5 ^a
<i>Ommatoiulus sabulosus</i>	48 $\pm$ 0.6 ^{ab}	106.8 $\pm$ 15.4 ^a	3010 $\pm$ 1101 ^a	0.58 $\pm$ 0.07 ^a	29.9 $\pm$ 11.4 ^{ab}	0.09 $\pm$ 0.05 ^{ab}	2.2 $\pm$ 0.3 ^a	104.1 $\pm$ 13.8 ^{ab}
Faeces	43 $\pm$ 2.4	32.6 $\pm$ 6.9	95 $\pm$ 29	1.36 $\pm$ 0.23	3 $\pm$ 0.9	0.49 $\pm$ 0.13	0.4 $\pm$ 0.7	237.8 $\pm$ 62.2
<i>Isopoda</i>	43.5 $\pm$ 3 ^a	34.9 $\pm$ 8.5 ^a	105 $\pm$ 33 ^a	1.3 $\pm$ 0.28 ^a	3.1 $\pm$ 1 ^a	0.45 $\pm$ 0.14 ^a	0.8 $\pm$ 0.8 ^a	197.5 $\pm$ 34.4 ^a
<i>Diplopoda</i>	42.5 $\pm$ 1.6 ^a	30.4 $\pm$ 3.7 ^a	84 $\pm$ 20 ^b	1.42 $\pm$ 0.17 ^a	2.8 $\pm$ 0.7 ^a	0.53 $\pm$ 0.12 ^a	0.1 $\pm$ 0.2 ^b	278.2 $\pm$ 57.7 ^b
<i>Armadillo officinalis</i>	42.7 $\pm$ 4.5 ^a	39.4 $\pm$ 12.4 ^a	128 $\pm$ 32 ^a	1.16 $\pm$ 0.35 ^a	3.6 $\pm$ 1.5 ^a	0.36 $\pm$ 0.15 ^a	0.5 $\pm$ 0.7 ^a	194.2 $\pm$ 27.6 ^a
<i>Armadillidium vulgare</i>	44.5 $\pm$ 2.8 ^a	35.3 $\pm$ 4.2 ^{ab}	103 $\pm$ 32 ^{ab}	1.27 $\pm$ 0.16 ^a	2.9 $\pm$ 0.7 ^a	0.46 $\pm$ 0.1 ^a	1.6 $\pm$ 0.7 ^b	201.7 $\pm$ 44 ^a
<i>Porcellio laevis</i>	43.3 $\pm$ 1.4 ^a	30 $\pm$ 5.1 ^{ab}	85 $\pm$ 25 ^{ab}	1.48 $\pm$ 0.25 ^a	2.8 $\pm$ 0.6 ^a	0.54 $\pm$ 0.12 ^a	0.3 $\pm$ 0.3 ^a	196.6 $\pm$ 37.7 ^a
<i>Glomeris marginata</i>	41.7 $\pm$ 2.2 ^a	26.7 $\pm$ 2 ^b	78 $\pm$ 16 ^b	1.57 $\pm$ 0.13 ^a	3 $\pm$ 0.7 ^a	0.55 $\pm$ 0.11 ^a	0 $\pm$ 0 ^a	264.1 $\pm$ 56.1 ^{ab}
<i>Cylindroiulus caerulocinctus</i>	42.4 $\pm$ 1.2 ^a	31.4 $\pm$ 2.8 ^{ab}	80 $\pm$ 17 ^{ab}	1.36 $\pm$ 0.16 ^a	2.6 $\pm$ 0.5 ^a	0.55 $\pm$ 0.13 ^a	0 $\pm$ 0.1 ^a	306 $\pm$ 80.5 ^b
<i>Ommatoiulus sabulosus</i>	43.6 $\pm$ 0.8 ^a	33.1 $\pm$ 3 ^{ab}	94 $\pm$ 25 ^{ab}	1.33 $\pm$ 0.12 ^a	2.9 $\pm$ 0.7 ^a	0.49 $\pm$ 0.13 ^a	0.2 $\pm$ 0.2 ^a	264.4 $\pm$ 24.1 ^{ab}

Table S4.4 - ANOVA table of linear regression between faeces properties and macrodetritivore physiological traits.

	<i>Df</i>	<i>SS</i>	<i>F</i>	<i>pval</i>	<i>R</i> ² <i>adj</i>
CN	ns				
CP	ns				
NP					
T ~ Mass specific consumption rate	1	2.0	4.9	0.036	0.118
<i>Residuals</i>	28	11.4			
T ~ Mass specific faeces production rate	1	1.9	4.7	0.039	0.113
<i>Residuals</i>	28	11.5			
WHC	ns				

Table S4.5 - Species score on physiological trait PCA (mass-specific consumption, mass specific faeces production, fresh weight, diet diversity, assimilation rate)

		Axis 1	Axis 2
		<i>F</i> _{5,24} =12.5	<i>F</i> _{5,24} =1.1
Species identity effect of species score on PCA axis		<i>pval</i> <0.001	<i>pval</i> =0.315
		<i>R</i> ² <i>adj</i> =0.67	<i>R</i> ² <i>adj</i> =0.01
Species score	<i>Armadillo officinalis</i>	-1,4 ± 0,35 ^a	0 ± 0,64 ^a
	<i>Armadillidum vulgare</i>	1,72 ± 1,82 ^b	-0,43 ± 1,43 ^a
	<i>Porcellio laevis</i>	0,92 ± 0,52 ^b	-0,29 ± 1,53 ^a
	<i>Glomeris marginata</i>	-0,85 ± 0,47 ^a	0,25 ± 0,75 ^a
	<i>Cylindroiulus caerulocinctus</i>	1,2 ± 0,78 ^b	0,91 ± 1,04 ^a
	<i>Ommatoiulus sabulosus</i>	-1,59 ± 0,67 ^a	-0,43 ± 1,07 ^a
Trait contribution (%)	Fresh weight (g)	21.8	1.0
	Mass specific consumption	30.1	16.6
	Mass specific faeces production	33.7	1.9
	Diet diversity	13.2	23.4
	Assimilation	1.1	57.1

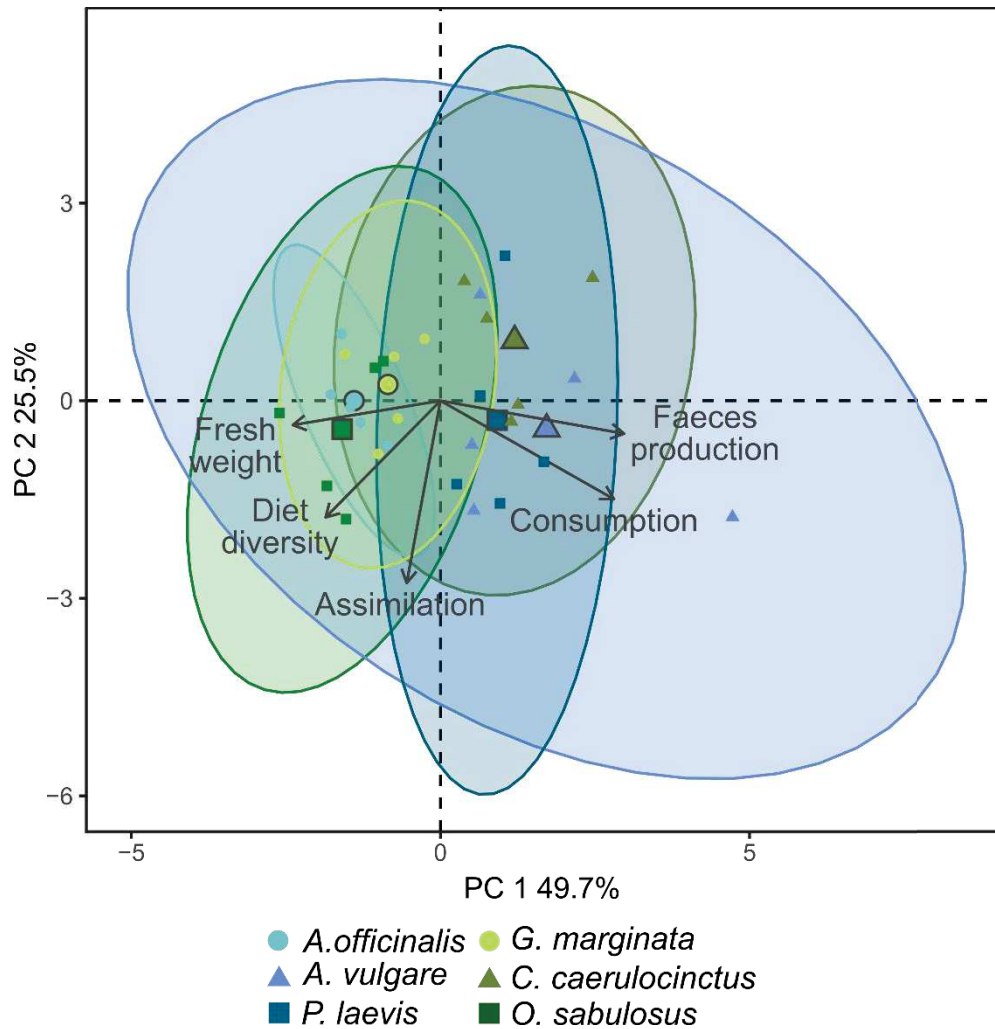


Figure S4.5 – Principal Component Analysis biplot on macrodetritivore physiological and morphological traits. Consumption= mass specific consumption rate ($\text{g.g}_{\text{fresh weight}}^{-1}.\text{day}^{-1}$), Faeces production = mass specific faeces production rate ($\text{g.g}_{\text{fresh weight}}^{-1}.\text{day}^{-1}$). Symbols and color define the six species, large symbols represent species 95% CI ellipse centroid. All traits were scale prior to ordination.

Chapter 4

Interactive effect of soil macrofauna and prolonged drought on nematode communities in an experimental Mediterranean forest

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Abstract

Climate change affects both soil processes and the interactions between organisms that drive these processes. While biodiversity at one trophic level promotes ecosystem processes and their resilience, less is known on the importance of multi-trophic biodiversity and biotic interactions, especially for soil organisms, and under changing environmental conditions. In a large-scale mesocosm experiment, we tested the hypothesis that increasing the functional diversity (FD) of soil and litter-feeding macrofauna (from a 12 species pool) would mitigate the effect of prolonged drought (30% longer drought duration) on nematodes, an important part of soil biota regulating microbial communities and processes. In addition the effect of specific macrofauna taxonomic groups were evaluated. Nematode communities were characterized by the relative abundance of taxonomic families and trophic groups, as well as proxies of the structure of soil food web. Prolonged drought negatively affected predator and omnivore nematodes proportion at the benefit of bacterivores, while macrofauna FD did not affect soil nematodes. Specific macrofauna taxonomic groups, however, had significantly impacts. Predator and omnivore nematodes increased in response to the activity of saprophagous millipedes, while the presence of endogeic ecosystem engineers (endogeic earthworms) considerably reduced nematode densities in general, at the expense of fungivore in particular, likely through passive ingestion and digestion of nematodes, the rupture of fungi hyphae or competition for microbial resource. Our results show how macrofauna alters soil micro food web and its response to climate change (longer drought), and call for the integration of multi-trophic interaction in the study of biodiversity – ecosystem functioning under changing climate.

Keywords

Biodiversity-ecosystem functioning, nematodes, earthworms, woodlice, millipede, climate change, food web, biotic interactions

5.1. Introduction

Climate change alter the species distribution (David and Handa 2010; Cardinale et al. 2012) and may ultimately alter the community composition and the interactions among organisms with cascading effects on ecosystem functions (Walther et al. 2002). Soils host a tremendous diversity of organisms with complex and multiple biotic interactions, including both trophic and non-trophic relationships (Wardle 2006). Despite the major role of soil organisms and networks in many ecosystem processes and services (Scheu 2002; Wall et al. 2012), very few is known about how climate change can alter interaction web in soils. Predicting ecosystem response to future global change therefore require deeper understanding of the link between different soil organism groups, and their response to multiple environmental changes (Bardgett and Wardle 2010; Blouin 2018).

Nematodes are the most abundant and widespread animals on earth (van den Hoogen et al. 2019). They also occupy a remarkable diversity of trophic niches, with bacterivore, fungivore, predator, omnivore, and plant-feeders nematodes organized in a soil micro-food web (Bongers and Bongers 1998; Ferris 2010). Microbial grazers, such as nematodes, consume microorganisms and therefore accelerate nutrient release rates into the soil (soil microbial loop; Coleman, 1994), with positive consequences for plant growth (Ingham et al. 1985; Wardle 1999). They are in strong interaction with other groups of soil biota, in particular macrofauna such as earthworms and saprophagous macrofauna (Lavelle and Spain 2001; Scheu 2002; Blouin 2018).

Soil macrofauna affect nematodes through 1) direct predation, 2) modification of nematode resources, i.e. microbial (bacterial or fungal), and 3) modification of nematode habitat, i.e. soil physical properties such as porosity and moisture. Earthworms ingest large quantities of soil and consequently also ingest nematodes that are then digested by the proteolytic enzymes in earthworms' gut, serving as amino acid source (Pokarzhewskii et al. 1997; Edwards 2004; Monroy et al. 2008). Nematode predation by earthworms can therefore result in strong decrease from 30 to 70% of nematode abundance (Dash et al. 1980; Yeates 1981; Hyvönen et al. 1994; Rätty and Huhta 2003; Dionísio et al. 2018). However, the transformation of litter in casts and the redistribution of organic matter in the soil profile by earthworms promotes bacterial over fungal communities and may result in more abundant nematodes communities,

notably bacterivore nematodes (Roessner 1986; Senapati 1992; Winding et al. 1997; Ilieva-Makulec and Makulec 2007). Furthermore, earthworms' burrowing activity modifies soil porosity and creates many suitable habitats for nematodes both in burrow walls and fresh casts due to their high moisture level, microbial activity and enhanced pore space (Elliott et al. 1980; Tiunov et al. 2001; Savin et al. 2004; Gorres and Amador 2010; Andriuzzi et al. 2016). To a lesser extent than earthworms, saprophagous macroarthropods and especially millipedes also dig burrows into the soil to avoid dry conditions at the surface and can therefore enhance soil porosity (David and Handa 2010). In parallel, the transformation of litter in fecal pellets by saprophagous macroarthropods and the resulting increase of organic matter quality (such as lower C:N ratio in the faeces) may also induce a positive effect on bacterial communities and therefore bacterivore nematodes (Bastow 2012). However the interactions between saprophagous macroarthropods and nematodes are far less studied (see Bastow 2011) compared to earthworms.

Natural macrofauna communities are composed of several species that have a specific feeding behavior, digestive enzyme equipment and faeces production rate and characteristic (Chapitre 3; Zimmer et al. 2002b, 2004b; Hedde et al. 2005). These species-specific attributes explain a species role in soil processes such as litter mass loss, rather than just its presence (Vos et al. 2011; Bílá et al. 2014). In mixed communities, the rate of litter mass loss and microbial activity increase only in the low end of a species richness gradient before reaching a plateau due to species functional redundancy, while they increase more steadily with functional diversity (FD), i.e. the variety and difference in the trait of species present in the assemblage (Cragg and Bardgett 2001; Heemsbergen 2004; Zimmer et al. 2005; Hedde et al. 2010; Coulis et al. 2015b; Lubbers et al. 2020). While soil macrofauna FD is recognized as a determining factor in soil microbial activity, its impact on soil microfauna has never been studied. However, if macrofauna FD tends to promote microbial processes, and notably bacterial-based ones, we can expect that nematodes communities, and especially bacterivore nematodes, would benefit from more active and abundant microbial communities, through a bottom-up effect (Scheu 2002).

Precipitation regime is also an important factor for nematode communities (Yeates 1979; de Vries et al. 2012; Sylvain et al. 2014). Free-living soil nematodes move and feed in the water

films on soil (micro)aggregates and are capable of anhydrobiotic cryptobiosis when conditions are too dry (Wharton 1986; Coleman et al. 2004) and can survive in small patches of moisture (enclosure hypothesis; Neher et al. 1999). Moreover, nematode response to drought is taxon and trophic group dependent, with predator group being generally more sensitive because of their different life strategy (low reproduction rate, large size, longer generation time) (Ferris et al. 2001), and fungal-based food webs being more resistant but less resilient than bacterial-based ones (de Vries et al. 2012). Several studies manipulated precipitation, usually reducing or increasing the amount of rainfall with transparent rain interception systems and artificial irrigation over a season to several years. These studies reported conflicting results with either negative, positive, or neutral effects of drought on soil nematode abundance, depending on nematode trophic group (see Table 1 for literature synthesis). The potential effect of drought on nematodes seem to follow changes in microbial communities, i.e. bottom-up control of the soil micro food web (Schnürer et al. 1986; Landesman et al. 2011; Stevnbak et al. 2012). Finally, our knowledge on the effect of different environmental conditions on the interactions between macrofauna and nematodes is still very limited. Nevertheless, few studies tested the effect of different precipitation regimes on the effect of macrofauna FD on soil processes. A FD positive effect on litter mass loss and microbial activity may be only visible at low soil moisture levels (Collison et al. 2013) due to increased complementarity in stressed condition (stress gradient hypothesis; Yachi and Loreau 1999). Conversely, this effect can be independent of rainfall frequency (Coulis et al. 2015b) as macroarthropod activity may be less affected by water limitation than microbial activity (Coulis et al. 2013b; Thakur et al. 2018).

Despite the acknowledged preponderant role of soil micro and macrofauna in soils, our knowledge on their interactions, especially in changing climatic conditions, remains limited. The few existing studies differ strongly in their experimental conditions, limiting comparison, and generally are too unrealistic, which can lead to biased results and limits generalization (refs). Indeed, most studies testing earthworm-microfauna interaction used small quantities of soil, with high earthworm densities, in absence of plant, without source of organic matter (litter), and in constant and favorable soil moisture conditions (Ellenby 1944; Dash et al. 1980; Senapati 1992; Hyvönen et al. 1994; Rätty and Huhta 2003). This prevents from capturing the functional domain of soil organisms and soil engineers (*sensu* Lavelle 2002) by ignoring

macrofauna effects on soil physical properties, water fluxes and on organic matter quality and availability and overestimates certain effect of soil biota on soil processes (Ganault et al. submitted; Blouin et al. 2005). Here, we propose to fill this gap by studying the soil nematode communities of an experimental Mediterranean forest mixed understory subjected to different precipitation regimes and hosting soil macrofauna communities of either high or low functional diversity (FD). We made the first hypothesis that (H1) prolonged drought periods would decrease total nematode abundance, with a stronger effect on higher trophic level nematodes (predators and omnivores) but will benefit the stress-tolerant microbial feeding nematodes. We also supposed that (H2) higher macrofauna FD will promote more diverse and abundant nematode communities, notably bacterivores, and (H3) would mitigate the drought impact on nematode communities. Finally, we hypothesized that (H4) ecosystem engineers (lumbricid earthworms) will have a stronger effect on nematode communities compared to litter transformers (diplopods and isopods) due to the more profound changes in soil properties, resource availability and quality that they induce.

5.2. Material and methods

5.2.1. Soil and mesocosms

Soil originated from the ECOTRON – CNRS of Montpellier experimental field (43°68'N, 3°88'E) and is composed, in the first 5 to 15cm, of 30 % of clay, 34 % of silt, 20.1 g.kg⁻¹ of organic matter, has a C:N ratio of 10.2, and a pH_{H2O} of 8.2 (Table S5.1). Soil excavation (40 tons) took place between the 18th and 19th of January 2018 by first removing the first 5 cm of vegetation and roots and sequentially excavate the first 10 cm (L1), 10 to 30 (L2) and 30 to 80 cm layers (L3) of the soil. Large rocks were removed by hand and soil was stored in big bags before sterilization. Soil from the first two layers (L1 and L2) was subjected to gamma radiation at low dose (2.5 kGy) to preferentially kill meso- and macrofauna while keeping microbial and nematodes communities less affected (McNamara et al. 2003). End of February 2018, soil was inserted in 16 lysimeters (1 m deep and 1m in diameter, ca. 1 Mg of soil each) and 10 cm deep layer of gravel (2-6 mm diameter) was added to ensure water drainage. Soil from L3 was added in six successive layers of 10 cm compacted to 1.4 g.cm⁻³, followed by two layers of 10cm of L2 soil compacted to 1.3 g.cm⁻³, and finally by one L1 layer of 10 cm compacted to 1.2 g.cm⁻³.

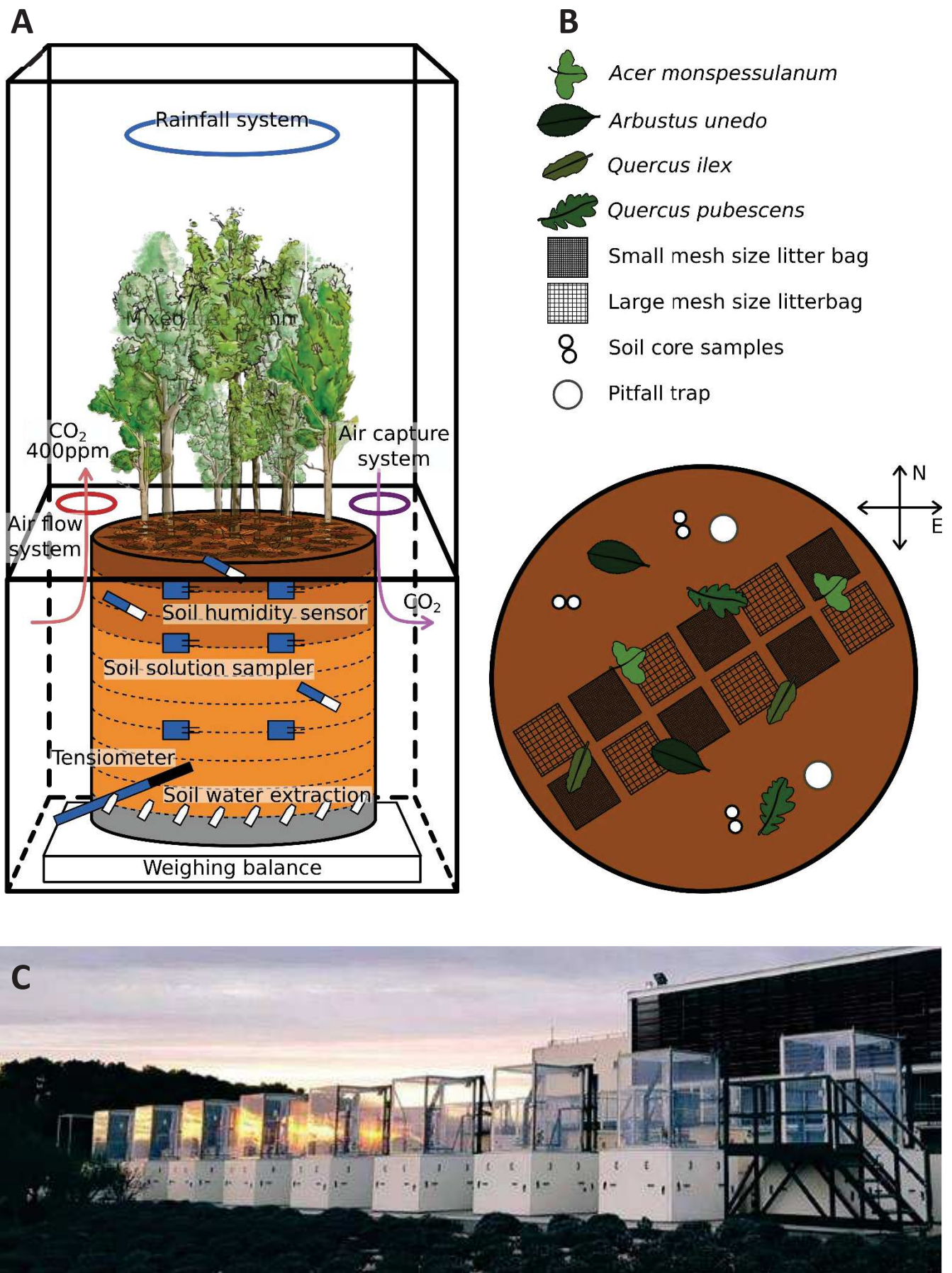


Figure 5.1 – Experimental mesocosms with **A-** lysimeter and mesocosm system, **B-** lysimeters soil surface design, and **C-** a view of all mesocosm at the ECOTRON CNRS experimental site.

Soil humidity sensor (TDR), soil solution sampler, tensiometers, and soil water extraction system were added during this step (Fig. 5.1A). The 16 mesocosms are arranged in two parallel rows aligned in an east-west that constitute two random blocks. Each mesocosm cover was highly transparent to light and UV radiation (250 µm thick Teflon- FEP film, DuPont, Wilmington, Delaware, USA) and allowed the soil surface and canopy of the lysimeters to be exposed to natural sunlight. Automatically controlled feedback loop algorithms based on industrial-grade proportional-integral-derivative (PID) controllers were used to achieve the desired set-points for air temperature, air humidity, and air CO₂ pressure (400 ppm). Daily meteorological conditions (excluding the drought treatment period) were based on the precipitation and temperature data recorded at the Puechabon experimental forest site from 2002 to 2017. A reference year was chosen (2013) as the year having the daily precipitation and temperature patterns the closest to average values across the 15 years of climatic data. These climatic conditions were maintained identical in all mesocosms outside the drought period.

5.2.2. Biological material

Four tree species representative of typical Mediterranean forests were selected namely *Acer monspessulanum* L. 1753 (Aceraceae), *Arbustus unedo* L. 1753 (Ericaceae), *Quercus ilex* L. 1753 (Fagaceae), *Quercus pubescens* Willd. 1796 (Fagaceae). These species are often found in mixed forests, and strongly differ in their chemical and physical traits, mycorrhizal type, leaf lifespan and litterfall phenology. Two years old saplings of the four tree species were bought from Pépinière BRL nursery (pepiniere.brl.fr), roots were thoroughly washed to remove soil, and two seedlings per species were planted from 7th to 9th of March 2018 in each lysimeter so each tree species had an equal light exposure (Fig. 5.1B). *Q. ilex* saplings exhibited a high mortality rate and were then replaced in February 2019 by other saplings obtained from acorns collected at the Puechabon experimental site.

Leaf litter was collected with suspended litter traps and from the ground at the tree species litterfall peak. Litter material was collected in different forests located nearby Montpellier (Table S5.2) and dried at 60 °C for 72 hours to kill any macro or mesofauna invertebrates. In July 2018, 62.5 ± 0.1 g of dry litter composed of each tree species entire leaves were added in each mesocosm. In June 2019 a second batch of manually fragmented litter was added below

the entire leaf layer and resulted in the addition of 29.9 ± 0.2 g of *A. unedo* and *A. monspessulanum* each and 75.2 ± 0.2 g of the two *Quercus* species each³. Soils were re-inoculated in March and December 2018 to improve microbial, mycorrhizal, and nematode community settlement. Soil of O and A horizon was collected in a mixed forest composed of *Q. ilex*, *Q. pubescens* and *A. unedo* (Montarnaud, France) where part of the biological material comes from. The inoculum was prepared by mixing 1 volume of soil to 5 volumes of deionized water and manually mixed for 30 min. The solution was passed through a 100 μ m sieve and then each mesocosm was homogeneously watered with 5l of this inoculate.

Table 5.1 - Macrofauna insertion events and community composition of the low and high functional diversity treatments. Number of individuals and total biomass (mean $\pm$ se). L. = Lumbricids. Individuals and biomass ($\text{g}_{\text{fresh weight}}$) expressed by m^2 .

Group	Species	First insertion		Second insertion		Community #							
		individuals	biomass	individuals	biomass	1	2	3	4	5	6	7	8
Isopoda	<i>A. vulgare</i>	28.0 ± 1.4	4.1 ± 0	27.5 ± 1	4.0 ± 0	x						x	
Isopoda	<i>A. officinalis</i>	20.8 ± 2.2	4.0 ± 0	19.8 ± 2.5	4.0 ± 0	x						x	
Isopoda	<i>P. laevis</i>	35.3 ± 1.9	4.1 ± 0	30 ± 4.3	4.1 ± 0.2			x				x	
Diplopoda	<i>C. cylindroiulus</i>	37.5 ± 1.7	4.0 ± 0	47 ± 1.6	4.0 ± 0.1			x				x	
Diplopoda	<i>G. marginata</i>	23.5 ± 1.7	4.1 ± 0.1	22.5 ± 2.4	4.0 ± 0.1				x			x	
Diplopoda	<i>O. sabulosus</i>	29.0 ± 1.4	4.0 ± 0.1	15 ± 2.9	4.1 ± 0.1	x						x	
L. endogeic	<i>A. caliginosa</i>	27.3 ± 1.9	13.4 ± 0.3	27.2 ± 0	15 ± 0		x						x
L. endogeic	<i>A. chlorotica</i>	66.5 ± 5.8	13.5 ± 0	42.8 ± 0	15 ± 0				x				x
L. endogeic	<i>A. icterica</i>	18.0 ± 0.8	13.6 ± 0.1	21.4 ± 0	15 ± 0	x							x
L. anecic	<i>A. nocturna</i>	4.0 ± 0	13.6 ± 0.6	4 ± 0	15.7 ± 0.6		x			x			
L. anecic	<i>S. gigas</i>	2.0 ± 0	13.2 ± 2.3	2 ± 0	16.2 ± 1			x		x			
L. anecic	<i>L. terrestris</i>	2.0 ± 0	12.8 ± 0.5	4 ± 0	15.6 ± 0.6				x	x			
						High FD				Low FD			

³ At the moment of adding the second litter batch, it was not possible to gather enough litter of *A. unedo* and *A. monspessulanum* of the required decomposition stage. Additionally, high litter production of *A. monspessulanum* in the mesocosms likely compensated for the unequal manual litter input for this species.

Macrofauna species pool consisted of the three woodlice (Isopoda: Oniscidae) *Armadillidium vulgare* Latreille 1804 (Armadillidae), *Armadillo officinalis* Duméril 1816 (Armadillidae), and *Porcellio laevis* Latreille 1804 (Porcellionidae), the three millipedes (Myriapoda: Diplopoda) *Glomeris marginata* Villiers 1978 (Glomeridae), *Cylindroiulus caerulocinctus* Wood 1864 (Julidae), and *Ommatoiulus sabulosus* (L. 1758), the three endogeic earthworms (Annelida: Lumbricidae) *Aporrectodea caliginosa* (Savigny, 1826), *Aporrectodea icterica* (Savigny, 1826), and *Allolobophora chlorotica* (Savigny, 1826), and the three anecic earthworms *Aporrectodea nocturna* (Evans, 1946), *Lumbricus terrestris* (L. 1758), and *Scheroteka gigas* (Dugès, 1828). Arthropods were collected by litter hand sorting in different forests surrounding the city of Montpellier and earthworms were hand sorted from soil in an orchard except *S. gigas* that was collected in the ECOTRON experimental field (Table S5.2). After collection, individuals were stored separately in a dark cold room (9 °C) in plastic boxes with a mix of the four litter species (arthropods) and in 30 cm deep bucket filled with a mix of experimental soil and soil of origin with a mix of the four litter on top (earthworms).

5.2.3. Functional diversity and drought treatments

As functional diversity metrics strongly depend on which traits are considered, the choice of species traits that are relevant for the considered ecosystem processes (effect traits) and/or reflect the species response to environmental conditions (response traits) is critically important. Although the trait-based approaches in soil fauna biodiversity studies are receiving a growing interest (Brousseau et al. 2018b; Wong et al. 2019), the identification of relevant traits that can encompass distant phylogenetic groups and include their multiple direct and indirect effects on ecosystem processes remains a challenging task. The few existing studies manipulating soil macrofauna FD have used different trait combinations on a wide range of macrofauna species mixtures (Heemsbergen 2004; Hedde et al. 2010; Coulis et al. 2013b; Lubbers et al. 2020) In our study, the low number of replicates within each precipitation regime treatment (n=8) was a strong practical constraint limiting the number of feasible different artificial communities and therefore values of FD. This led us to aim for a treatment with two levels of FD (low or high), replicated four times each. Instead of using a trait based approach, we have used phylogenetic diversity as a proxy of functional diversity by mixing phylogenetically distant groups (earthworms vs woodlice vs millipedes), based on the

assumption that phylogenetic distances between these groups would capture their functional responses and roles (Webb et al. 2002; Brousseau et al. 2018a) and allow us to maximize functional differences without a deep insight into the relevant traits. We assembled low FD communities composed of species of the same group (only woodlice, or millipede, or earthworm species, Table 5.1), and high FD communities composed of species of different groups (one woodlice, one millipede, and one earthworm species). The earthworms group included two clearly distinct ecological categories, the anecic and the endogeic earthworms (Bottinelli et al. 2020b) that were considered separately in our design. The species richness was kept constant and equal to three species across all the communities and all possible group combinations were assembled (Table 5.1). To select communities composition among all possible group combination, we followed a “constrained random sampling design” (Heemsbergen 2004) meaning that the different levels of FD were achieved with different species composition and each individual species occurred the same number of time in each FD modalities (Table 5.1). The 5th of December and the 12th of April 2019, 4 g of each arthropod species and 13 g of each earthworm species were inserted in the mesocosm (Table 5.1). To assess the establishment of all species, we sampled the individuals from the mesocosms by first removing the litter and hand sorting it the 21st of May 2019, and collected pitfall traps that were open for two days with a moist tissue inside (Fig. 5.1B). After an overnight precipitation, earthworm communities were sampled by electric extraction. Sampled animals were identified, weighed, and put back into the mesocosm of origin within 12 hours.

The drought treatment consisted in increasing hydric stress duration. In mesocosms exposed to prolonged drought period, rainfall events were determined as a function of the control mesocosm soil water potential (SWP). The hydric stress duration was defined as the time spent at SWP between -1MPa and above -1.5MPa. When SWP approached -1.5MPa in control mesocosms after a period without rainfall, control mesocosms were re-watered while this hydric stress duration was extended by 30% for mesocosms of the drought treatment (Fig. S5.2). This led to impose 3 drought events to the mesocosms (Fig. S5.2) of that treatment before applying the same climatic conditions on all mesocosms again. This precipitation regime led to soil moisture at 10cm deep 2.7% drier in the drought treatment compared to the control mesocosms ($F = 7.9$, $pval = 0.014$, Table S5.2). However, the mesocosm showed

individual hydric behavior with some drying faster or slower, leading somewhat to mesocosms from the prolonged drought treatment with soil moisture values higher than mesocosms from the control treatment. To account for this mesocosm variability, we also used values of soil moisture at 10cm deep as a co-variable by calculating the daily-mean soil moisture value across the whole drought period (1st of August to 13rd of October 2019).

5.2.4. Nematodes extraction and community indices

In each mesocosm, three sampling points were determined and two soil cores (8cm deep, 5cm wide) were collected in each sampling point. From the two soil cores, ~70g of fresh soil was taken for nematode extraction by manually gently crushing the soil cores, while the rest of the soil core was sieved to 4mm and kept for further microbial analysis⁴ and measurement of soil water content (on ~10g fresh mass). Nematodes were extracted with the decanting plus sieving plus sucrose-centrifugation method (details in Appendix 5.1; Jenkins 1964). Abundances were expressed as individuals per gram of dry soil. Subsamples were then pooled and nematodes identified to the family level, used to calculate community diversity (Hill's diversity of order 1, see Chapter 1). Information of family individual body weight was used to estimate total biomass of nematodes (Ferris 2010). Nematodes families were then classified into different functional guilds (Ferris et al. 2001) based on their *colonizer-persister* classes (Bongers and Bongers 1998) and feeding types (Yeates et al. (1993): plant feeders (Pl_x), fungivores (Fu_x), bacterivores (Ba_x), predator (Pr_x), and omnivores (Om_x), with x the c-p class ranging from 1 to 5 (Table 5.2). We then computed the Enrichment Index (EI), Structure Index (SI) and Nematod Channel Ratio (NCR) (Ferris et al. 2001; Yeates 2003). EI is calculated as below:

$$EI = 100 \times \frac{Ba_1 + Fu_2}{Ba_1 + Ba_2 + Fu_2} \quad (1)$$

and provides information on the resource status of the ecosystem with low values when the system is nutrient limited. Using nematodes of higher c-p values from c-p 3 to c-p 5, i.e. nematodes in systems with more stable conditions, the SI gives a description of how structured and how numerous trophic links are in the soil micro food-web. It is calculated as

⁴ DNA, PLFA, Denitrification Enzyme Activity, Substrate-Induced Respiration

$$SI = 100 \times \frac{Ba_{3-5} + Fu_{3-5} + Pr_{3-5} + Om_{3-5}}{Ba_{3-5} + Fu_{3-5} + Pr_{3-5} + Om_{3-5} + Ba_2 + Fu_2} \quad (2)$$

and high value indicates a complex and well-structured food-web that is more resistant and resilient to perturbations (Ferris et al., 2001). Herbivores nematodes are classically removed from these index calculations because they react differently to nutrient availability (Bonger and Bongers, 1998). Finally, NCR indicates the relative contribution of bacterivore and fungivore nematodes to total nematode abundance (Yeates et al., 2003). It is calculated as

$$NCR = 100 \times \frac{Ba}{Ba + Fu} \quad (3)$$

where Ba and Fu are bacterivore and fungivore nematodes of all c-p classes, respectively. High value of NCR indicates bacterial-mediated community, and therefore bacterial dominated microbial processes in the soil. All family-level information and food-web indices were computed with the NINJA automated calculation system (Sieriebriennikov et al. 2014).

Table 5.2 - List of nematode families identified and associated code for NMDS representation (Fig 5.2), c-p class, feeding type, assigned functional guild, individual mass, total density and frequencies.

Feeding type	C-p class	Family	Code	Functional guild	Individual mass (μg)	Total density (ind.g ⁻¹ dry soil)	Relative abundance (%)
Bacterivore	1	Rhabditidae	Rhabd	Ba1	5.037	0.10	0.6
	2	Osstellidae	Osste	Ba2	0.230	4.4	24.4
	2	Cephalobidae	Cepha	Ba2	0.408	3.97	22.0
	2	Plectidae	Plect	Ba2	0.845	0.94	5.2
	3	Prismatolaimus	Prism	Ba3	0.413	0.50	2.8
Fungivore	2	Aphelenchoididae	Aphel	Fu2	0.191	1.79	9.9
	4	Tylencholaimidae	Tylencho	Fu4	1.411	0.01	0.1
Omnivore	4	Qudsianematidae	Qudsi	Om4	2.233	0.61	3.4
	4	Dorylaimidae	Doryl	Om4	12.838	0.03	0.2
	5	Aporcelaimidae	Aporc	Om5	22.727	0.33	1.8
Predator	3	Tripylidae	Tripy	Pr3	3.488	0.07	0.4
	4	Nordiidae	Nordi	Pr4	2.619	1.01	5.6
	4	Anatonchidae	Anato	Pr4	6.749	0.29	1.6
	4	Mononchidae	Monon	Pr4	5.268	0.19	1.1
	4	Mylonchulidae	Mylon	Pr4	1.734	0.03	0.2
Plant-feeders	2	Tylenchidae	Tylenchi	PI2	0.160	3.58	19.9
	3	Hoplolaimidae	Hoplo	PI3	0.527	0.07	0.4
	3	Dolichodoridae	Dolic	PI3	0.601	0.06	0.3
	3	Pratylenchidae	Praty	PI3	2.136	0.01	0.1
	5	Longidoridae	Longi	PI5	13.526	0.04	0.2

5.2.5. Statistical analysis

Difference in nematode family composition between treatments (high or low FD, ambient or prolonged drought) was tested by PERMANOVA (*adonis* function from *vegan* package) on the Bray-Curtis dissimilarity matrix and results were visualized with non-Metric Dimensional Scaling. All analyses were done with the R software version 3.5.2 (R Development Core Team, 2019). Changes in micro food-web structure was represented with the ternary plot of the proportion of Cp1, Cp2 and Cp3-5 nematodes, and with the EI-SI quadrats graph (Ferris et al. 2001). Nematode community structure was assessed with the following metrics: abundance, biomass, diversity, and proportion among free-living nematodes (except for plant feeders) of feeding groups and Cp classes. We constructed a first model where we tested the effect of macrofauna FD and precipitation regime and their interaction by two-way ANOVA. In a second step, the effects of FD and of the presence of each macrofauna group (anecic earthworm, endogeic earthworm, woodlice, and millipede) were tested all in interaction with daily-average soil moisture. For each modelling step, model selection was done with the *dredge* function (MuMIn package) by keeping the best models within a ΔAIC of 2, and rejecting all models if the null model was included.

5.3. Results

5.3.1. Nematode community composition and structure

Nematode communities were composed of 20 different families of the five possible feeding type and C-p class (Table 5.2). Osstellidae, Cephalobidae, and Tylenchidae represented 24.4, 22, and 19.9% of the community, respectively. On the opposite, nine families were present in very low abundance, each constituting less than 1% of the community. Cephalobidae, Osstellidae, Plectidae, Anatonchidae, and Mononchidae were the only families to occur in all mesocosms. Community composition was affected by the precipitation regime (Fig. 5.2, Table S5.3). Rhabditidae and Dorylaimidae only occurred in mesocosms exposed to ambient drought, while Mylonchulidae and Dolichodoridae only occurred under prolonged drought condition (Table S5.4). Prolonged droughts also reduced the dissimilarity between

communities from the different mesocosms as shown by smallest distance between each mesocosm and the barycenter of its treatment (Fig. 5.2).

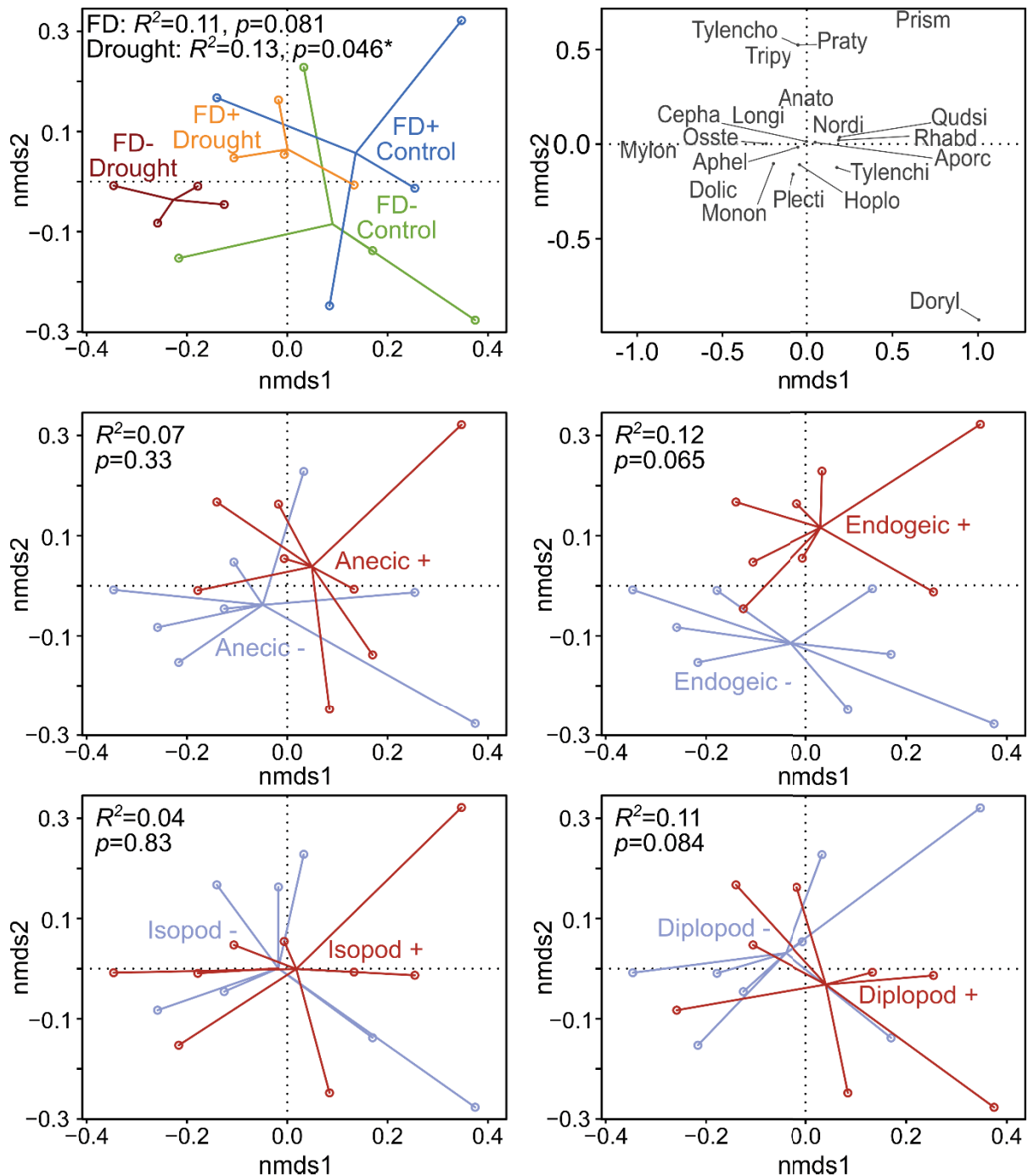


Figure 5.2 – nMDS biplot of the nematode community dissimilarity matrix (Bray-Curtis). Spider groups representing the treatment (FD+/- = high/low functional diversity, Drought = prolonged drought, Control = ambient drought), or the presence (+) and absence (-) of the different macrofauna groups (anecic earthworm, endogeic earthworm, isopod, and diplopod). Family codes are detailed in Table 2. R^2 and p value in top left corner are PERMANOVA tests.

Macrofauna FD marginally affected nematode community composition while the effect of prolonged drought appeared more clearly in the low FD treatment (Fig. 5.2, Table S5.3). The presence of endogeic earthworms and diplopods marginally affected family composition while anecic and isopod presence did not. More precisely, endogeic earthworm presence induced the disappearance of Aphelenchoididae and Qudsianematidae but promoted the establishment of Aporcelaimidae, Nordiidae, Tripylidae, Longidoridae, and Tylenchidae. Conversely, diplopod presence promoted Aphelenchoididae, Aporcelaimidae, Nordiidae, and Tylenchidae, while preventing the installation of Qudsianematidae population. On average, nematodes were present in lower densities ($1.13 \pm 0.38 \text{ ind.g}_{\text{dry soil}}^{-1}$) than in Puechabon experimental site soil from which the inoculum was prepared ($16.7 \text{ ind.g}_{\text{dry soil}}^{-1}$, Homet Gutierrez P. *pers comm*). Nematode density strongly decreased (-35.8%) in the presence of endogeic earthworms and this effect was also observed for the density of fungivore and Cp2 nematodes (Table 5.3). Nematode diversity or biomass were not affected by the experimental treatments, but were the lowest under prolonged drought with low macrofauna FD (Table 5.3).

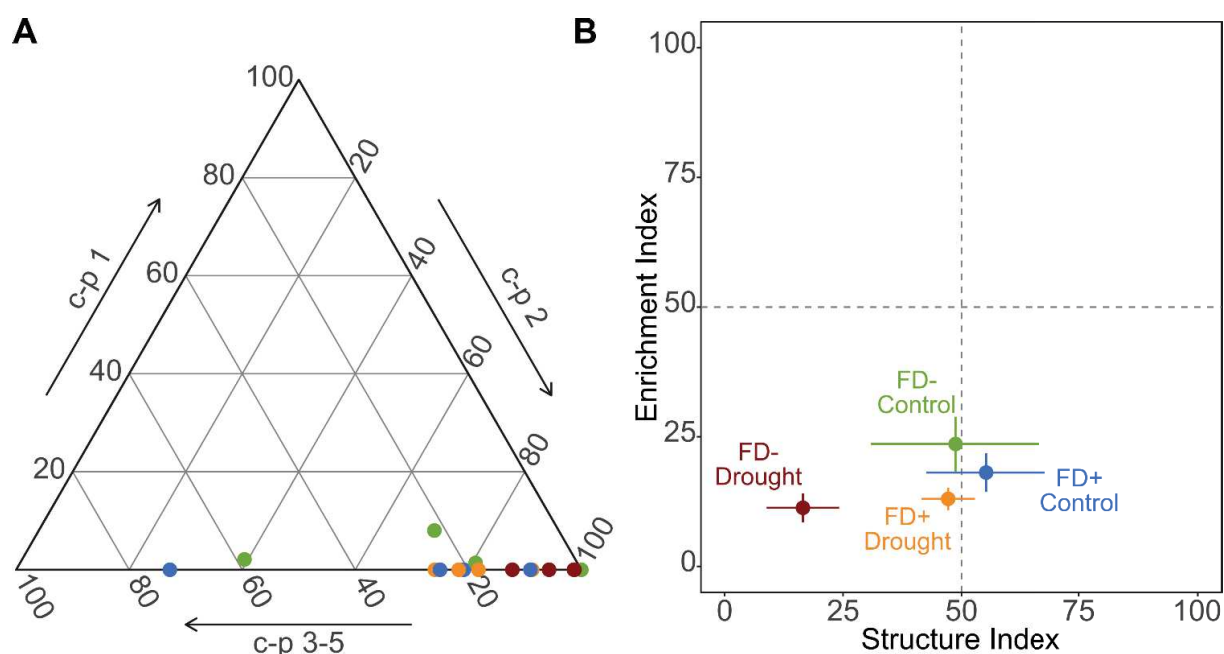


Figure 5.3—A. Cp triangle and B. Enrichment Index (EI) and Structure Index (SI) trajectories for mesocosms exposed to different treatment (FD+/- = high/low functional diversity, Drought = prolonged drought, Control = ambient drought). In B, points represent the mean index value of the treatment, bars are standard error.

Table 5.3 - ANOVA table of the best models testing first the effect of precipitation regime (control or prolonged drought) and functional diversity (low or high fd), and then the presence/absence of each macrofauna group (anecic earthworms, endogeic earthworms, isopod, and diplopod) in interaction with averaged daily soil moisture at 10cm during the precipitation manipulation period. Ba = bacterial feeders, Fu = fungal feeders, Om = omnivores, Pr = predators, Pl = plant feeders, CPX = c-p classification, EI = Enrichment Index, SI = Structure Index, NCR = Nematod Channel Ratio Index. *ns*= no significant effect detected, *na*= non applicable (too many zeros). d = density (ind.g_{dry soil}⁻¹), % = relative proportion in the community. The four right columns indicate the mean ± se values of each index in the crossed treatment precipitation regime x macrofauna FD.

Y	Predictor	Df	SS	F	pval		F-D+	F+D+	F-D-	F+D-
Density	endogeic	1	0.2	11.2	0.005	↓	1.2 ± 0.3	0.9 ± 0.2	1.3 ± 0.5	1.2 ± 0.5
Diversity	ns						4.3 ± 1	6.2 ± 1.3	6 ± 1.8	5 ± 0.7
Biomass	ns						0.12 ± 0.14	0.15 ± 0.06	0.32 ± 0.28	0.15 ± 0.08
Ba%	drought	1	480.7	3.8	0.071	↑	82.7 ± 10.6	70.4 ± 3	64.1 ± 18.5	67.1 ± 4.6
Ba%	diplopod	1	562.9	7.3	0.018	↓				
	moisture	1	678.1	8.8	0.011	↓				
Ba d	ns						0.85 ± 0.18	0.52 ± 0.09	0.56 ± 0.26	0.55 ± 0.18
Fu%	ns						12.2 ± 6.3	12.9 ± 4.6	11.3 ± 6.4	15.2 ± 10
Fu d	endogeic	1	0.02	4.1	0.062	↓	0.14 ± 0.11	0.1 ± 0.04	0.1 ± 0.08	0.11 ± 0.07
Pr%	ns						3.8 ± 4	10.6 ± 5	14.4 ± 14.8	11 ± 8.9
Pr d	ns						0.05 ± 0.07	0.08 ± 0.05	0.17 ± 0.22	0.1 ± 0.1
Om%	ns						1.4 ± 1.6	6.1 ± 4	10.3 ± 10.3	6.7 ± 4.2
Om d	ns						0.02 ± 0.02	0.05 ± 0.03	0.13 ± 0.16	0.05 ± 0.03
Pr + Om %	diplopod	1	3.5	4.5	0.053	↑	0.07 ± 0.09	0.13 ± 0.05	0.3 ± 0.37	0.14 ± 0.09
	moisture	1	3.9	5.1	0.043	↑				
Pr + Om d	ns						5.13 ± 5.18	16.73 ± 5.42	24.65 ± 24.57	17.7 ± 7.28
Pl%	ns						10.8 ± 4.6	14.8 ± 9.3	25.4 ± 22.7	27.5 ± 23.2
Pl d	ns						0.12 ± 0.03	0.14 ± 0.09	0.32 ± 0.29	0.36 ± 0.42
CP1%	na						0 ± 0	0 ± 0	2.9 ± 3.5	0 ± 0
CP1 d	na						0 ± 0	0 ± 0	0,02 ± 0,02	0 ± 0
CP2%	drought	1	1274	3.6	0.078	↑	94.9 ± 5.2	81.4 ± 7.3	72.5 ± 25.4	68.1 ± 28.1
CP2 d	endogeic	1	1.02	14.8	0.002	↓	1,08 ± 0,24	0,73 ± 0,16	0,95 ± 0,37	0,91 ± 0,6
CP3-5%	drought	1	1076	3.1	0.101	↓	5.1 ± 5.2	18.6 ± 7.3	24.6 ± 24.5	31.9 ± 28.1
CP3-5 d	ns						0,09 ± 0,11	0,16 ± 0,08	0,3 ± 0,36	0,26 ± 0,23
EI	drought	1	302	5.9	0.03	↓	11.3 ± 5.6	13 ± 4.3	23.6 ± 10.6	18.1 ± 7.5
EI	moisture	1	460.3	11.5	0.004	↑				
SI	ns						16.5 ± 15.3	47.2 ± 11.3	48.8 ± 35.7	55.2 ± 25.2
NCR	ns						86.7 ± 7.2	84.5 ± 5	86 ± 5.5	81.7 ± 11

5.3.2. Nematode functional structure and food web properties

“cp2” bacterivores dominated the community (51.6%) while fungivore nematodes represented on average 10% of the community, leading to an average NCR of 0.85, i.e. the dominance of the bacterial channel over the fungal channel. Plant-feeding nematodes were the second most abundant trophic group, almost only represented by Tylenchidae Omnivore and predator were present in relatively low proportion, constituting 5.4% and 8.9% of the total community, respectively. Soil moisture reduced bacterivore nematodes proportion (estimate $\pm$ se = -2.83 ± 0.96) that was also negatively influenced by millipede presence (-11.9%). The presence/absence of endogeic earthworms significantly altered the fungivore density, with a reduced fungivore density and virtually no Aphelenchoididae (Fu2) in the presence of endogeic earthworms. Combined, predators and omnivores’ proportion increased with soil moisture and marginally in presence of diplopods (Table 5.3, Fig. 5.4). Overall, mesocosm under prolonged drought with low macrofauna FD tended to have the lowest proportion and density of predator, omnivore, and plant feeder nematodes, while the opposite pattern was observed under ambient drought with low macrofauna FD treatment (Table 5.3). Nematodes of Cp1 were almost absent from the system, only represented the bacterivore Rhabditidae family, with a relative abundance of 0.6%. Communities facing prolonged drought in the low macrofauna FD treatment had the lowest nematodes of Cp3 to 5, more of Cp2, and therefore less structured and communities (Fig 5.3B & 5.4, Table 5.3). Prolonged droughts led to lower EI, which logically strongly increased with soil moisture. NCR was the lowest (higher proportion of fungivore) under ambient drought regime and high macrofauna FD, but the difference was not significant.

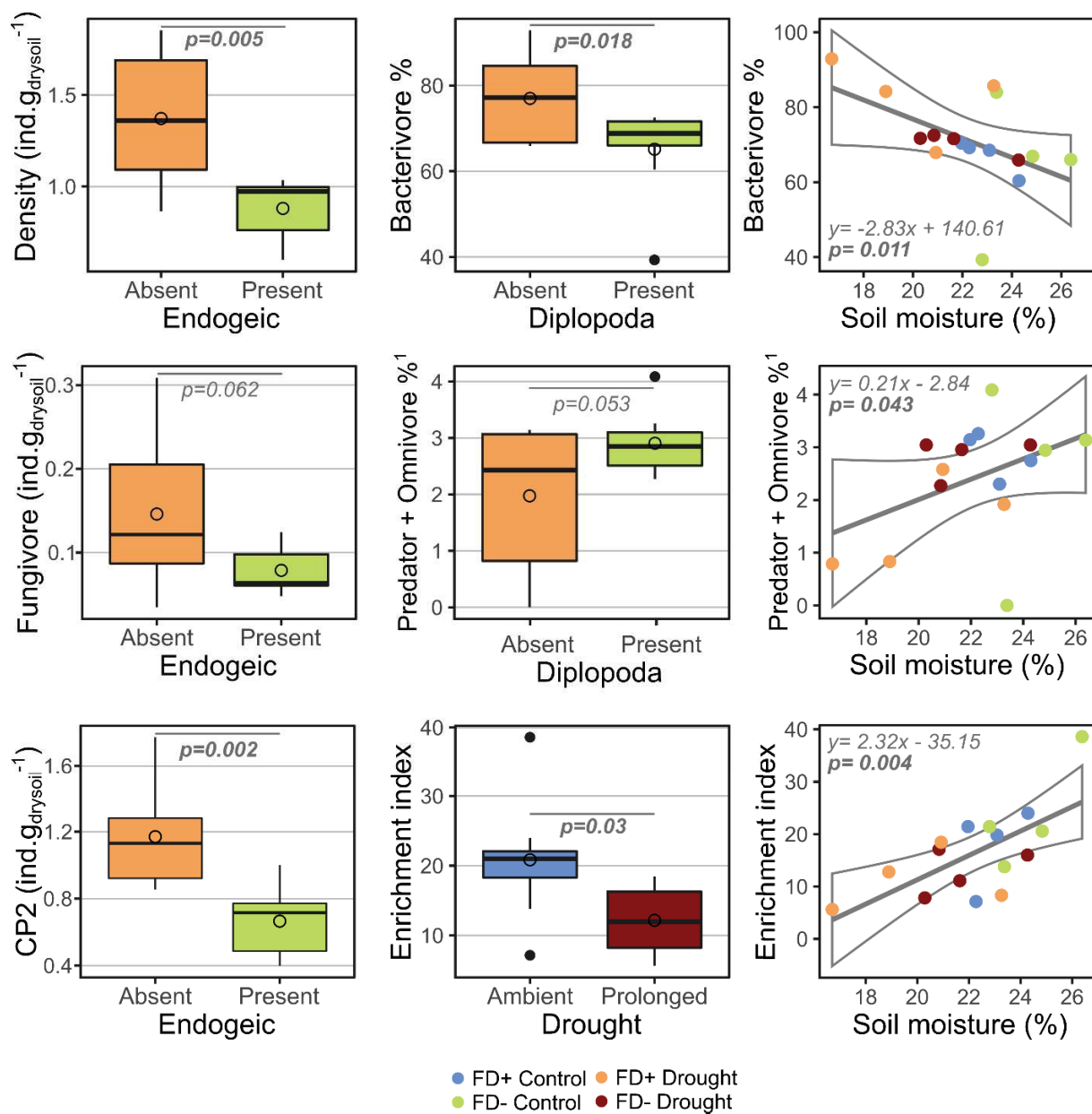


Figure 5.4 – Boxplot and linear regressions illustrating selected relationships modelled (Table 3). ¹data log(1+x) transformed.

5.4. Discussion

We studied the joint effect of soil macrofauna functional diversity and prolonged drought on soil functioning and soil micro food web by characterizing nematode communities in large-scale experimental mesocosm reproducing a Mediterranean mixed forest understory ecosystem. Prolonged drought, and associated reduced soil moisture, induced strong changes in the community composition, with reducing the proportion of predator and omnivore nematodes, to the benefit of bacterivores. Albeit marginal, macrofauna FD affected nematode community composition, and reduced the prolonged drought effect on enrichment and structure index of the micro food web. Additionally, endogeic earthworms decreased total nematode density and more specifically fungivore and Cp2 nematodes density, while millipede presence induced higher proportion predator and omnivore compared to bacterivore.

5.4.1. Drought effect on community composition and food web structure

The prolonged drought induced only small reduction in daily soil water moisture at 10cm deep, but it was strong enough to significantly affect nematode community composition as we stated in our first hypothesis, showing the high sensibility of these small organisms and their potential to inform on ecosystem response to global changes (Landesman et al. 2011). By increasing drought duration, daily mean soil water content at 10cm over summer was lower and reduced the proportion of predators and omnivores to the benefit of bacterial feeding nematodes. This pattern can be explained by the fact that nematodes of higher trophic ranks exhibit high cp values with long lifetime, low fecundity and larger body size. These nematodes are more sensitive to environmental perturbation than microbial feeders (Bongers and Bongers 1998), and corroborates the results of other studies in different ecosystems (Sylvain et al. 2014; Siebert et al. 2019). Additionally, while the soil moisture diminishes, large pores dry faster than small pores, limiting first the movement of larger bodied taxa such as predators that will have less access to their resource (Strong et al. 2004; Erktan et al. 2020). The released top-down predation pressure on bacterivore may have therefore allow their increase in the community, highlighting the importance of considering different trophic level to understand

soil biota response to environmental changes (Scheu 2002; Bastow 2011; Blouin 2018; Xiong et al. 2020).

It is interesting to note that several studies reported no or very limited effects of drought on soil nematodes communities despite stronger changes in soil moisture than in our study (Freckman et al. 1987; Papatheodorou et al. 2004; Eisenhauer et al. 2012; Cesarz et al. 2015; Thakur et al. 2018; Siebert et al. 2019). Most of these studies were conducted on sites with sandy soils, where water drainage is higher due to the higher soil porosity compared to soil with high silt and clay content, as in our study. Nematodes community living in sandy soils are likely adapted to more fluctuating water availability and therefore are less sensible to precipitation regime manipulation (Papatheodorou et al. 2004; Eisenhauer et al. 2012). Additionally, only few studies reported nematode response to precipitation modification in forest ecosystems despite the fact that drought has consistent negative effect on soil biota, regardless of taxonomic group and size class, only in forest ecosystems (Blankinship et al. 2011). The observed increasing ratio of bacterivores to omni-predators nematodes with drought are however in opposition to the only studies done in forest ecosystems that found lower bacterivore abundance under drought (Landesman et al. 2011) and lower abundance of omnivore and predator under increased rainfall and N-enrichment (Sun et al. 2013). Difference in the study site properties, i.e. mixed pine-oak forest on sandy acidic soil with a history of wild and controlled fires in Landesman et al. (2011) and mixed broad-leaved – pine forest on Eutric cambisol developed from volcanic ash and temperate continental monsoon climate in Sun et al. (2013), may result in different nematode community adaptation to precipitation modification. These inconsistent results stress the need to investigate nematodes community response to altered precipitation in more diverse ecosystems.

5.4.2. Macrofauna functional diversity mitigates drought effects on soil micro food web

The effect of macrofauna FD was only marginal after 10 month of experiment but coherent tendencies started to emerge, with more structured micro food web with high macrofauna FD under prolonged drought conditions. Increased structure suggest increased connectivity in the micro food web and therefore higher resistance of the whole community (Bongers and Bongers 1998; Ferris et al. 2001). In presence of functionally diverse macrofauna communities,

soil porosity and organic matter quality and spatial availability likely increased in more different ways due to the complementarity of species-specific burrowing and feeding activity of earthworms and arthropods (Hedde et al. 2005; Capowiez et al. 2015). Pursuing the monitoring of nematodes communities in this experiment will allow us to see if this trend strengthen with time.

However, some limitations must be addressed to explain why macrofauna FD had less impact than individual macrofauna groups (see next section). The absence of significant effect may be first explained by the method we used to construct the FD treatment, based on the strong assumption that ecologically and/or phylogenetically distant groups would also be functionally different. Although phylogenetic distance (PD) does capture evolutionary differences linked to a species adaptation to and effect on its environment (Webb et al. 2002), PD and FD are not always related, and PD may be a poorer predictor of ecosystem processes than FD (Flynn et al. 2011; Pavoine et al. 2013). Secondly, it is possible that the mean functional characteristic of the community (Community Weighted Mean, CWM) rather than its functional diversity matters to quantify macrofauna effect in soils, as suggested by the mass-ratio hypothesis (Grime 1998). Few studies tested the relative importance of FD and CWM in soil processes since these two indices are mathematically related (Dias et al. 2013). Studying isopods effect on litter mass loss, Bílá et al. (2014) showed that CWM was a better predictor than FD. The fact that individual macrofauna group presence or absence (endogeic earthworm and millipede) influenced nematode communities may give further support for the importance of community composition and species identity for ecosystem processes (Heemsbergen 2004; Hedde et al. 2010; Lubbers et al. 2020). Future trait measurement on the species used in our experiment and the calculation of different functional metric (FD and CWM) will help us to better interpret these results.

5.4.3. Effects of individual macrofauna groups

The presence of endogeic earthworms (in three-species mixture or represented by one species with other macrofauna species) induced a strong decrease in nematode density, notably of fungivore nematodes. It can be due to three mechanisms: nematodes consumption, selective feeding on fungi, and competition for organic matter and microbial communities. First,

endogeic earthworms create vast burrow systems and ingest larger quantities of soil than anecic earthworms (Capowiez et al. 2015). In our case, *Aporrectodea icterica* may have played a particular role in soil bioturbation as this particular species produced more numerous and longer burrows resulting in higher bioturbation than the other two species *Aporrectodea caliginosa* and *Allolobophora chlorotica* (Capowiez et al. 2015). This intense burrowing activity may lead to higher passive nematode ingestion by earthworm with strong consequences for soil micro food web (Dash et al. 1980; Monroy et al. 2008; Dionísio et al. 2018). On the opposite, anecic earthworms create fewer, vertical and (semi)permanent burrows (Capowiez et al. 2015), which leaves larger volume of soil undisturbed, and allow nematodes to establish themselves at vicinity of the burrow walls (Tiunov et al. 2001; Savin et al. 2004; Andriuzzi et al. 2016). Anecic earthworms therefore have smaller functional domain volume, and this may explain the absence of effect of this group on nematodes in our study, especially since we never sampled soil with anecic burrows in it, while it happened that some endogeic earthworm individuals were found in the samples. Secondly, decrease in fungivore nematodes may be explained by negative effect of earthworm on fungi communities. Fungi can constitute a major food source for earthworms (Brown 1995; Bonkowski et al. 2000) and be digested during the passage through earthworm gut (Wolter and Scheu 1999). In addition, soil bioturbation may break fungi hyphae and limit their development (Brown et al. 2004a). Future PLFA and DNA analysis on the soil samples will inform us on whether the fungal communities were affected or not. Finally, as earthworm ingest microorganisms, they can compete for food with bacterivore and fungivore nematodes and negatively affect their populations (Elliott et al. 1980; Rätty and Huhta 2003).

The presence of millipedes increased predator and omnivore proportion over bacterivore nematodes. Millipedes can not only improve organic matter quality through their feeding activity, but they can also change soil structure by producing faecal pellets of different particle size than leaf litter and incorporate them passively in the soil while burrowing in the first few centimeters (Anderson 1988b; Dangerfield and Chipfunde 1995). This may improve soil structure, increase soil porosity, nutrient availability and favor nematode trophic interactions (Erktan et al. 2020). If predator and omnivore nematodes benefited from improved habitat characteristics, they likely exerted a stronger top-down control on bacterivore nematodes,

reducing their proportion in the community (Allen-Morley and Coleman 1989; Mikola et al. 1998; Bastow 2011).

Conclusion

Both prolonged drought and macrofauna community composition affected soil micro food web with potential consequences for ecosystem functioning. The increase in bacterivore proportion in response to drought may exert top-down control on bacterial communities and alter the response of microbial communities and associated soil processes to prolonged drought. The action of different soil macrofauna group induced a strong decrease in nematode density or restructuring of nematode communities. Our result first confirms the importance of macrofauna for the microfauna communities, but also show that community composition rather than functional diversity influence soil food web. Biotic interactions are therefore underpinning soil processes and should be further considered in studies investigating the role of soil organisms and their diversity on ecological processes under different environmental conditions (Eisenhauer et al. 2019b).

Supplementary information

Table S5.1 - Soil properties at the different depth L1 (5-15cm), L2 (15-35cm) and L3 (35-85cm).

	L1	L2	L3
clay %	30.3 ± 0.4	28.2 ± 0.6	13.3 ± 1
silt %	33.7 ± 0.4	35 ± 3.2	30.6 ± 2.1
sand %	36.6 ± 0.7	41.6 ± 5	71.9 ± 24.3
N g/kg	1.1 ± 0	1 ± 0	0.4 ± 0.1
C:N	10.2 ± 0.2	9.7 ± 0.4	8.9 ± 1.1
Ca g/kg	35.5 ± 24.7	41 ± 28.5	48.5 ± 33.8
Corg g/kg	11.6 ± 0.3	9.3 ± 0.4	3.8 ± 1.1
Mg g/kg	1 ± 0.8	1 ± 0.8	1.2 ± 1
Mn mg/kg	13 ± 0.5	13 ± 0.7	6.2 ± 0.8
MO g/kg	20.1 ± 0.6	16 ± 0.7	6.5 ± 1.9
pH _{H2O}	8.2 ± 0	8.3 ± 0	8.5 ± 0
K g/kg	0.4 ± 0.2	0.3 ± 0.1	0.3 ± 0.1

Table S5.2 – Biological material sampling site information

	Site of collection	Coordinates	Method of collection
Tree species			
<i>Acer monspessulanum</i>	Mas d'Arnaud	43°60'N, 35°9'E	Litter traps
<i>Arbustus unedo</i>	Montarnaud	43°39'N, 3°40'E	Ground collection
<i>Quercus ilex</i>	Puechabon	43°44'N, 3°35'E	Litter traps
<i>Quercus pubescens</i>	CEFE-TE	43°63'N, 3°86'E	Litter traps
Detritivore species			
<i>Armadillidium vulgare</i>	Montarnaud	43°39'N, 3°40'E	Litter hand sorting
<i>Armadillo officinalis</i>	ECOTRON	43°68'N, 3°88'E	Litter hand sorting
<i>Porcellio laevis</i>	CEFE-TE	43°44'N, 3°35'E	Litter hand sorting
<i>Glomeris marginata</i>	Montarnaud	43°39'N, 3°40'E	Litter hand sorting
<i>Cylindroiulus caerulocinctus</i>	Montarnaud	43°39'N, 3°40'E	Litter hand sorting
<i>Ommatoiulus sabulosus</i>	Marseille	43°36'N, 3°42'E	Litter hand sorting
<i>Aporrectodea caliginosa</i>	Avignon	43°9'N, 3.88'E	Soil hand sorting
<i>Aporrectodea icterica</i>	Avignon	43°9'N, 3.88'E	Soil hand sorting
<i>Allolobophora chlorotica</i>	Avignon	43°9'N, 3.88'E	Soil hand sorting
<i>Aporrectodea nocturna</i>	Avignon	43°9'N, 3.88'E	Soil hand sorting
<i>Lumbricus terrestris</i>	Avignon	43°9'N, 3.88'E	Soil hand sorting
<i>Scheroteka gigas</i>	ECOTRON	43°68'N, 3°88'E	Soil hand sorting

Figure S2 – Watering events in the control and drought treatment mesocosms.

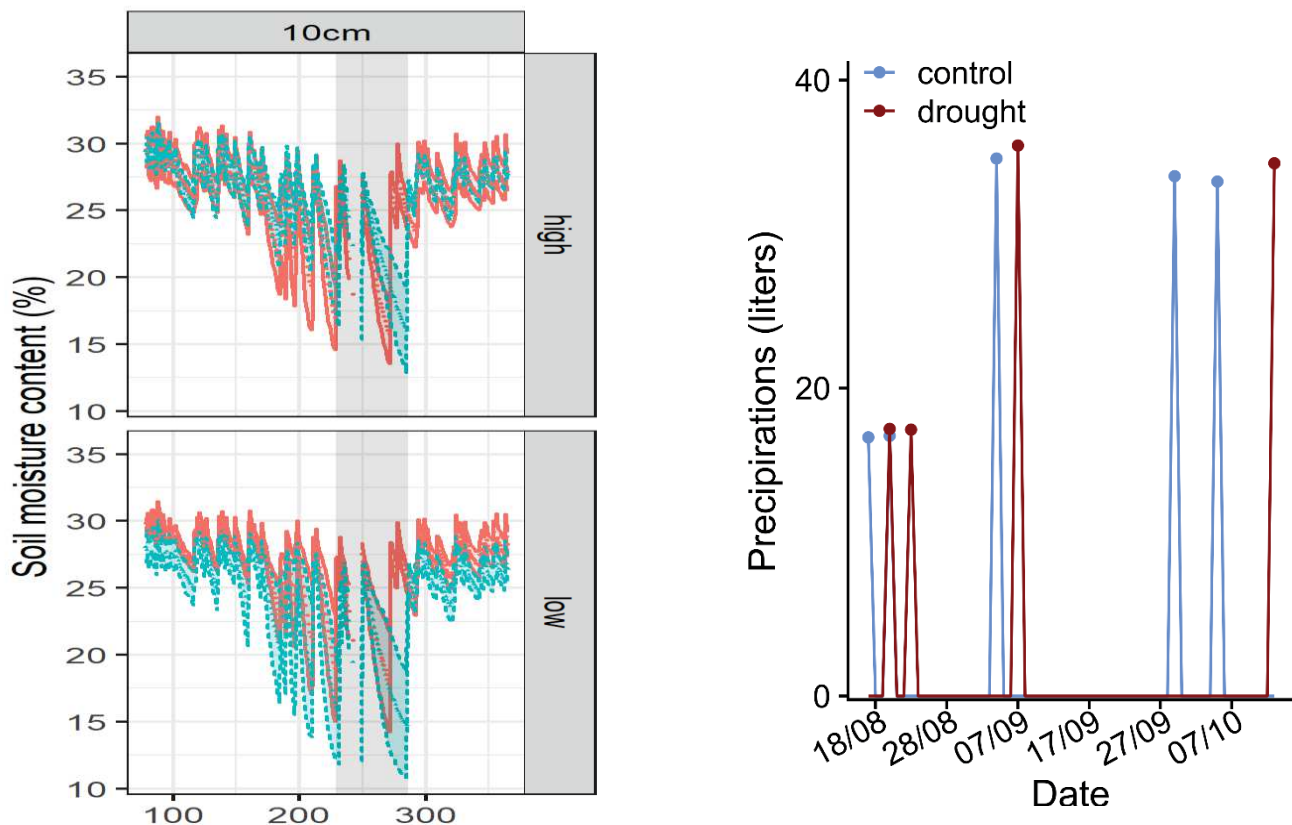


Figure S5.2 – Watering events in the control and drought treatment mesocosms.

Appendix 5.1 – Free-living soil nematodes extraction procedure.

~70g of fresh soil was weight to the nearest 0,1g and mixed into 1L of tap-water by gently disaggregating soil particles with a stick during 1min and then let sediment for 10min. The solution was mixed again for 30 sec, let sediment for 30 sec and then passed through two sieves of 180 and 38 μ m mesh size. The content retained by the 38 μ m sieve was collected in 50mL Falcon tubes. Each falcon was then cetrifugated at 3000rpm, 25°C for 10minutes. Supernant water was removre and replace by a sugar-solution at 45%. Tubes were then re-centrifugated at 3000rpm for two minutes, supernatent was pased through a 25 μ m seive, rinsed with tap water, and retrieved in a 10mL tubes. After nematodes counting with a stereoscope, samples were stored over night at 4°C to let nematodes sediment. The day after, 8 of the 10 mL were removed from the tube and replaced by a 4% formaldéhyde solution at 60°C and stored again at 4°C before identification under microscope.

Table S5.3 - PermANOVA table of nMDS ordination of nematod dissimilarity matrix

Variable	Df	SS	F	R ²	pval
FD	1	0.2	1.8	0.11	0.081 †
Drought	1	0.2	2.2	0.13	0.046 *
FD:Drought	1	0.1	0.8	0.05	0.599
<i>Residuals</i>	<i>12</i>	<i>1.3</i>		<i>0.72</i>	
Anecic	1	0.1	1.1	0.07	0.332
<i>Residuals</i>	<i>14</i>	<i>1.7</i>		<i>0.93</i>	
Endogeic	1	0.2	1.8	0.12	0.063 †
<i>Residuals</i>	<i>14</i>	<i>1.6</i>		<i>0.88</i>	
Isopod	1	0.1	0.6	0.04	0.831
<i>Residuals</i>	<i>14</i>	<i>1.7</i>		<i>0.96</i>	
Diplopod	1	0.2	1.7	0.11	0.084 †
<i>Residuals</i>	<i>14</i>	<i>1.6</i>		<i>0.89</i>	

Table S5.4 - Nematode family occurrence in the different treatments. Plus signs indicate family occurrence while empty cells indicate family absence.

Family	Guild	%	Drought		Control		Anecic		Endogeic		Isopod		Diplopod	
			FD-	FD+	FD-	FD+	-	+	-	+	-	+	-	+
Cephalobidae	Ba2	22	+	+	+	+	+	+	+	+	+	+	+	+
Osstellidae	Ba2	24.4	+	+	+	+	+	+	+	+	+	+	+	+
Plectidae	Ba2	5.2	+	+	+	+	+	+	+	+	+	+	+	+
Prismatolaimus	Ba3	2.8		+		+	+	+	+	+	+	+	+	+
Rhabditidae	Ba1	0.6			+		+		+	+	+		+	+
Aphelenchoididae	Fu2	9.9	+	+	+	+	+		+		+			+
Tylencholaimidae	Fu4	0.1		+			+	+	+	+	+	+	+	+
Aporcelaimidae	Om5	1.8	+	+	+	+	+			+		+		+
Dorylaimidae	Om4	0.2			+		+	+	+	+	+	+	+	+
Qudsianematidae	Om4	3.4	+	+	+	+	+		+			+	+	
Anatonchidae	Pr4	1.6	+	+	+	+	+	+	+	+	+	+	+	+
Mononchidae	Pr4	1.1	+	+	+	+	+	+	+	+	+	+	+	+
Mylonchulidae	Pr4	0.2	+				+	+	+	+	+	+	+	+
Nordiidae	Pr4	5.6	+	+	+	+		+		+	+			+
Tripylidae	Pr3	0.4		+	+	+	+	+		+		+	+	+
Dolichodoridae	PI3	0.3	+				+	+	+	+	+	+	+	+
Hoplolaimidae	PI3	0.4	+	+	+	+	+		+	+	+	+	+	+
Longidoridae	PI5	0.2		+			+	+		+	+	+	+	+
Pratylenchidae	PI3	0.1		+			+	+	+	+	+	+	+	+
Tylenchidae	PI2	19.9	+	+	+	+		+		+	+			+
Total family richness			13	16	14	13	18	15	15	18	17	16	16	19

Discussion générale

6.1. Synthèse des résultats et validation des hypothèses

6.1.1. Structure des communautés de macrofaune du sol

6.1.1.1. Diversité et type fonctionnel des arbres

Hypothèse 1.1 : *l'abondance et la diversité de la macrofaune sont plus élevées en forêts mixtes que pures, car le mélange d'espèces augmente la probabilité d'inclure une espèce d'arbre aux traits favorables pour la macrofaune, et peut résulter en la mise à disposition d'habitats et de ressources plus diverses.*

Hypothèse 2.1 : *les parcelles de forêts mixtes fourniront davantage de microhabitats plus diversifiés et une qualité de litière en moyenne meilleure pour les proies des carabiques favorisant une plus grande proportion de généralistes d'habitat et régime alimentaire, et une plus grande diversité fonctionnelle.*

Hypothèse 2.2 : *la proportion d'arbres à feuillage persistant diminue la qualité du sol et de la litière, et la diversité de la végétation sous-arborée, réduisant la diversité fonctionnelle des carabiques pour favoriser les espèces spécialistes des forêts et zoophages. La diminution associée de fertilité du milieu induira une diminution de la taille moyenne des carabiques.*

Nous avons observé une plus grande richesse, diversité et équitabilité des Ordres de macrofaune du sol dans les peuplements mixtes que dans les peuplements monospécifiques (chapitre 1), mais cet effet ne persiste pas lorsqu'un niveau de résolution taxonomique spécifique est considéré pour décrire les communautés d'invertébrés et n'est pas observé à l'échelle spécifique (Chapitre 1 et 2). A l'inverse, la proportion d'arbres à feuillage persistant est associée à une diminution de la richesse, de la diversité et de l'équitabilité des Ordres, ainsi qu'à la biomasse de prédateurs (araignées et chilopodes, Chapitre 1) et à la taille corporelle moyenne des Carabidae (Chapitre 2). **Nos résultats confirment l'importance de la diversité des arbres, mais suggèrent que cet effet s'exprime différemment en fonction du**

niveau de résolution taxonomique considéré. De plus, nos résultats confirment l'importance du type fonctionnel des arbres (i.e. décidus/sempervirents) et plus précisément des arbres sempervirents, dont la présence entraîne une diminution de la qualité et augmentation de la quantité de la litière, ainsi que la fermeture de la canopée.

6.1.1.2. Conditions microclimatiques, habitat et ressources

Hypothèse 1.2 : *les communautés de macrofaune sont largement structurées par les conditions microclimatiques et de microhabitats, avec une augmentation attendue de l'abondance et de la diversité des communautés sous les arbres présentant une plus grande ouverture de la canopée permettant l'établissement d'une strate herbacée fournisseuse de microhabitats et de ressources diversifiés.*

Hypothèse 2.3 : *la fermeture de la canopée filtre pour les espèces spécialistes des forêts, incapable de voler (aptères ou brachyptères) et meilleures marcheuses (plus grande longueur de jambe par rapport à la longueur totale).*

Hypothèse 2.4 : *la qualité du sol, reliée à la productivité de la parcelle va positivement influencer la masse corporelle moyenne.*

Hypothèse 2.5 : *la biomasse et diversité de végétation sous arborée ainsi que la biomasse de proie potentielle à la surface du sol vont respectivement favoriser les espèces généraliste en favorisant les espèces graminivore, et les espèces zoophages.*

Les chapitres de résultats 1 et 2 montrent tout d'abord l'importance de la densité de la canopée pour la structuration des communautés : les forêts avec une canopée plus ouverte supportent une plus grande abondance d'espèces sapro-géophages (vers de terre, isopodes, diplopodes), une plus grande diversité de prédateurs (araignées, chilopodes et Carabidae), et exerce un important filtre sur les traits des Carabidae en favorisant les espèces capable de vol et généralistes d'habitat et de régime alimentaire. Nous avons mis en évidence que la quantité de litière est fortement et négativement reliée à l'abondance et la biomasse des organismes sapro-géophages qui constituent la majorité de la biomasse animale totale dans les échantillons de tri manuel de sol (notamment les vers de terre, Chapitre 1). **En accord avec notre hypothèse 1.2. 2.3-4-5, les conditions microclimatiques, et dans une moindre mesure**

les microhabitats, sont des facteurs explicatifs déterminants de l'abondance et de la diversité de la macrofaune.

6.1.1.3. Groupes trophiques et traits fonctionnels

Hypothèse 1.3 : *la réponse de la macrofaune dépend de son niveau trophique, et les organismes saprophages sont plus sensibles que les prédateurs aux changements de composition en arbres car ils sont plus directement reliés à eux que les prédateurs.*

Nous avons vu dans le chapitre 1 que les espèces sapro-géophages dépendent de la quantité et qualité de la litière, de même que certains groupes de prédateurs (araignées et chilopodes, mais pas les Carabidae). La structure fonctionnelle des Carabidae est de plus largement influencée par les caractéristiques du peuplement forestier et particulièrement de l'ouverture de la canopée et du type fonctionnel (Chapitre 2). **Ces résultats réfutent l'hypothèse 1.3 et montrent que les caractéristiques de la végétation sont des paramètres majeurs pour la structuration des communautés de macrofaune du sol quel que soit le groupe trophique considéré.**

6.1.2. Effet de la macrofaune sur la transformation de la matière organique et les communautés de microfaune du sol sous sécheresse prolongée

6.1.2.1 Préférences alimentaires des macroarthropodes saprophages

Hypothèse 3.1 : *les macroarthropodes saprophages préfèrent les litières riches en nutriments, pauvres en tannins, avec une capacité de rétention d'eau élevée et une faible épaisseur.*

Dans notre expérience en microcosme (chapitre 3), les macroarthropodes saprophages ont principalement consommé l'espèce de litière avec la concentration en nutriment la plus basse et la plus haute teneur en tannins. Cette espèce de litière présentait également le plus haut coefficient de tubularité et ses feuilles ont été clairement utilisées comme microhabitat durant l'expérience. La deuxième espèce de litière la plus consommée est par contre de haute qualité physico-chimique. **Contrairement à l'hypothèse 3.1, ces résultats montrent que les propriétés physico-chimiques ne suffisent pas à prédire les préférences alimentaires des macrodétritivores, et qu'en présence de mélange de litière en quantité non limitante, les espèces a priori les moins appétantes peuvent être malgré tout largement consommées.**

6.1.2.2. Transformation de la matière organique

Hypothèse 3.2 : *les propriétés des boulettes fécales dépendent de la composition du régime alimentaire des macroarthropodes, de leurs besoins nutritionnels et de leur capacité à digérer les constituants complexes de la litière (tannins). Ainsi, chaque espèce de macroarthropodes saprophages produira des boulettes fécales aux propriétés différentes et induira une transformation spécifique de la matière organique.*

Dans le Chapitre xx, nous avons démontré que par rapport au mélange de litière disponible, les boulettes fécales sont globalement plus riches en azote et en phosphore (ratios C/N et C/P plus bas), moins riche en tanins (dans 5 espèces étudiées sur 6), et ont une plus grande capacité de rétention d'eau. Des différences fines entre espèces de macrodétritivores sont cependant observables, mais elles ne s'expliquent pas directement par la composition du régime alimentaire. D'une façon générale, les isopodes produisent des boulettes fécales plus riches en azote et présentant une capacité de rétention d'eau plus basse que celles des diplopodes. **En accord avec l'hypothèse 3.2, les propriétés de boulettes fécales dépendent de l'identité du macrodétritivore, et ne sont pas prédictibles à partir de leur régime alimentaire.**

6.1.2.3. Réponse de la microfaune à la prolongation des sécheresses

Hypothèse 4.1 : *une sécheresse prolongée diminue l'abondance des nématodes, notamment aux plus hauts niveaux trophiques (prédateurs et omnivores), favorisant les nématodes microbivores plus résistants aux stress environnementaux.*

Avec une prolongation de 30% de la durée des épisodes de sécheresse, nous avons observé un changement dans la composition des communautés de nématodes avec une diminution de la proportion des nématodes prédateurs et omnivores, et une augmentation des nématodes bactériovores. La sécheresse prolongée a ainsi affecté le micro réseau trophique du sol, résultant en un réseau moins structuré. A l'inverse les nématodes fongivores et herbivores ne semblent pas affectés par la sécheresse, de même que l'abondance, la diversité ou la biomasse des nématodes en général, ou encore le ratio bactériovores/fongivores. **Ces résultats valident**

notre hypothèse 4.1 et montrent qu'une sécheresse même faible peut entraîner d'importants changements de structure du micro réseau trophique.

6.1.2.4. Importance de la diversité fonctionnelle de la macrofaune

Hypothèse 4.2 : *une macrofaune plus diversifiée fonctionnellement favorise l'abondance et la diversité des nématodes, notamment celles des bactérivores, et limite l'impact négatif de la sécheresse.*

La diversité fonctionnelle de la macrofaune n'a pas eu d'effet marqué sur les communautés de nématodes, mais a eu tendance à limiter les effets négatifs de la sécheresse sur la structure du micro réseau trophique. **Notre hypothèse 4.2 n'est donc que partiellement validée après seulement six mois d'expérimentation.**

6.1.2.5. Différents groupe fonctionnels de faune, différents effets sur la microfaune

Hypothèse 4.3 : *tous les groupes de macrofaune n'induiront pas la même réponse des nématodes avec un effet plus grand des ingénieurs de l'écosystème (vers de terre anécique et endogés) qui affectent le sol de façon plus importante et variée que les transformateurs de litière (isopodes et diplopodes).*

Dans notre expérimentation, les vers de terre endogés ont largement diminué la densité de nématodes, notamment de stratégie de vie cp2, alors que les diplopodes ont eu pour effet d'augmenter la proportion de nématodes prédateurs et omnivores, au détriment des nématodes bactérivores. Les vers anéciques et les isopodes n'ont par contre eu aucun effet. **Ces résultats réfutent l'hypothèse 4.3 et illustrent que les groupes fonctionnels classiquement utilisés (ingénieurs de l'écosystème et transformateurs de litière) ne sont pas toujours adaptés pour prédire leur effet sur les communautés du sol.**

6.2. Perspectives

Les forêts sont le siège de nombreux processus écosystémiques et sont d'importants réservoirs de biodiversité (Shvidenko et al. 2005; Bonan 2008). La macrofaune du sol dans ces écosystèmes est par ailleurs impliquée dans divers processus écologiques, notamment en affectant la dynamique de la matière organique et les autres organismes du sol (Lavelle 2002; Wall et al. 2012, cette thèse). Les forêts et les organismes du sol qui y habitent sont toutefois menacés par les changements climatiques comme les changements dans les régimes de précipitations ainsi que la destruction des habitats (Lindner et al. 2010; Blankinship et al. 2011; Cardinale et al. 2012). Face à ces risques, il est urgent de faire progresser nos connaissances sur les interactions entre communautés végétales et animales et comment ces interactions assurent le fonctionnement des écosystèmes face à diverses perturbations environnementales. Dans ce but, les résultats de cette thèse montrent dans un premier temps comment les communautés de macrofaune du sol se structurent dans les forêts européennes et quelles caractéristiques des arbres importent pour la diversité taxonomique et fonctionnelle des macroinvertébrés. Ces résultats permettent de formuler quelques recommandations sur la gestion de ces écosystèmes. Dans un second temps, les interactions biotiques entre litière végétale, faune sapro-géophage, et microfaune sont détaillées pour mieux comprendre la complexité des interactions entre ces trois compartiments qui régulent le fonctionnement des écosystèmes.

6.2.1. Vers une gestion forestière plus résiliente et protégeant la biodiversité

6.2.1.1. *Les forêts mixtes*

Indépendamment du contexte pédoclimatique, nos résultats montrent que les forêts plus diversifiées accueillent la même diversité spécifique et la même abondance de macrofaune du sol que les forêts monospécifiques, et qu'elles peuvent même favoriser la richesse, la diversité et l'équitabilité lorsque celles-ci sont mesurées à l'échelle des grands ordres de macrofaune (chapitre 1). Ces résultats confirment donc au moins partiellement l'importance de la diversité des arbres pour la diversité des communautés du sol, ce qui s'explique probablement par la mise à disposition simultanée d'une ressource en moyenne de meilleure qualité, ainsi que de microhabitats plus nombreux et diversifiés. Sur l'ensemble des parcelles

du projet FunDivEUROPE (dont font partie les 64 parcelles échantillonnées dans cette thèse), il avait déjà été démontré que la diversité des arbres (variant de 1 à 5 espèces) favorise la diversité des araignées, et de certains champignons ainsi que l'abondance des araignées et mammifères ongulés (Ampoorter et al. 2019). Cette thèse apporte donc davantage de support pour l'importance des mélanges d'arbres pour le maintien de la biodiversité forestière dans son ensemble.

En plus de favoriser la biodiversité, les peuplements mixtes sont également de plus en plus étudiés pour leur capacité à augmenter la résistance et résilience des écosystèmes forestiers à différentes perturbations. Conjointement à l'étude de la macrofaune, le projet SoilForEUROPE s'est intéressé à la diversité et aux fonctions microbiennes. En exposant les sols provenant des mêmes parcelles forestières à deux cycles de séchages / réhumectation en microcosme, Gillespie et al. (2020) ont montré que la résistance de la respiration microbienne était plus élevée dans les peuplements d'arbres mixtes. Par ailleurs, une récente méta-analyse a démontré l'effet positif de la diversité végétale sur la biomasse microbienne, dans des écosystèmes très variés (forêts naturelles, forêts plantées, prairies, cultures) (Chen et al. 2019). L'ensemble de ces résultats, obtenus sur une large diversité de sites, soutient l'intérêt des peuplements d'arbres mixtes pour le maintien de la diversité des organismes édaphiques et des processus écologiques auxquels ils participent, avec comme conséquence une plus grande résistance des forêts aux changements globaux (Scherer-Lorenzen et al. 2005).

6.2.1.2. La composition fonctionnelle

Les effets positifs globalement observés de la diversité spécifique des arbres sont toutefois à pondérer au regard de l'importance de la composition fonctionnelle des arbres (chapitre 1 et 2). En effet nos résultats montrent que les communautés de macrofaune sont plus largement influencées par la dominance des arbres à feuillage persistant, et les modifications de la qualité et de la quantité de litière qui en découlent. Ces résultats concordent avec les précédents travaux du projet FunDivEUROPE sur les vers de terre (De Wandeler et al. 2018) et plusieurs taxons dont les araignées (Ampoorter et al. 2019). De la même façon, les fonctions microbiennes ainsi que la diversité des guildes fongiques et des activités enzymatiques dans les sols des mêmes forêts ne semblent pas sensibles à la diversité des arbres, mais plutôt aux

traits des racines, notamment des racines absorptives et de leur degré de colonisation mycorhizienne (Gillespie et al. submitted; Prada-Salcedo et al. submitted). Ces résultats suggèrent qu'au-delà de favoriser le mélange d'espèce d'arbre par rapport aux forêts en monoculture, il est important de choisir les espèces constituant le mélange suivant les communautés ou fonction que l'on souhaite favoriser. A partir des 209 parcelles du projet FunDivEUROPE, Baeten et al. (2018) ont étudié l'effet de la diversité et de la composition des forêts sur la provision de 30 différentes fonctions et services écosystémiques (recyclage des nutriments, productivité primaire, régénération, résistance aux perturbations, provision d'habitats) et la multifonctionnalité des forêts. Cette étude montre que les peuplements les plus productifs (et donc intéressants pour la sylviculture) montrent également un haut niveau de multifonctionnalité et qu'il est possible d'identifier des espèces d'arbre favorisant cette multifonctionnalité au sein de chaque type de forêts (hémi-boréale : *Picea abies*, hêtraie : *Fraxinus excelsior*, forêts décidues thermophiles : *Quercus ilex* et *Q. cerris*, forêts méditerranéennes : *Pinus sylvestris*) (Baeten et al. 2018). Ces résultats témoignent des progrès encourageants réalisés dans notre compréhension du rôle de la composition spécifique des forêts pour le maintien de leur fonctionnement à l'avenir.

6.2.1.3. Gestion de la structure du peuplement forestier

Cette thèse a étudié des forêts matures où l'activité humaine est basse comparée à d'autres systèmes dans lesquels la gestion humaine peut être plus présente, ceci dans le but de maintenir une production de produits sylvicoles maximale. Il existe quatre types principaux de pratiques de gestion des forêts en régénération naturelle : 1) l'entretien au stade jeune de la forêt par la réduction de la densité de tiges et la sélection des espèces, 2) l'élimination des arbres les moins beaux, et l'élagage du houppier des arbres maintenus dans les peuplements plus matures, ceci dans le but de limiter la compétition pour la lumière, 3) la récolte d'arbres, avec maintien des semenciers, créant des zones ouvertes de différentes dimensions plus ou moins homogènes à large échelle, et 4) la régénération naturelle et/ou la plantation de nouvelles pousses pour remplacer les zones ouvertes et potentiellement changer la composition spécifique. Ces différentes pratiques sont déterminantes pour les interactions entre individus et espèces d'arbres, et donc pour les mécanismes de coexistence qui sont à la base de la réalisation des processus écologiques (Cordonnier et al. 2018). L'entretien et la

régénération vont être primordiaux pour déterminer la composition du peuplement, pendant que l'élagage et la coupe vont fortement affecter la structure du couvert forestier qui est un des paramètres les plus importants pour la structure taxonomique et fonctionnelle des communautés de macrofaune (chapitre 1 et 2). L'ouverture de la canopée semble influencer positivement les organismes du sol et notamment les macro-prédateurs, probablement du fait de l'augmentation de la température au sol qui favorise l'activité de ses organismes (Mueller et al. 2016). A l'inverse, l'ouverture de la canopée induit de forts changements dans la composition et la couverture de la végétation sous arborée, pouvant limiter la diversité de la macrofaune sapro-géophage (Henneron et al. 2015; Mueller et al. 2016). L'effet de la structure de la canopée sur la macrofaune dépend du groupe considéré et suggère que l'élagage et l'exploitation des arbres doivent être précautionneusement planifiées pour ne pas drastiquement affecter certains groupes de la macrofaune du sol. Ce type de gestion et son effet sur le microclimat doivent être d'autant plus étudiés qu'il a été montré que l'influence de l'identité des arbres sur les conditions microclimatiques affecte fortement le processus de décomposition de la matière organique (Joly et al. 2017; Gottschall et al. 2019). L'ensemble des parcelles du projet FunDivEUROPE ont été récemment équipées de sondes microclimatiques qui permettront une meilleure description de ces mécanismes dans les projets à venir.

6.2.2. Appréhender la diversité de la macrofaune du sol

Décrire la diversité taxonomique et fonctionnelle de la macrofaune du sol est toujours un défi. Historiquement, les organismes ont été classés dans différents groupes (écomorphologiques, trophiques, de taille, fonctionnels...) afin de simplifier cette diversité, et de faciliter l'étude de certains groupes particuliers considérés comme stratégiquement importants du fait de leurs liens reconnus avec des fonctions précises dans l'écosystème. Ces approches, si elles ont permis de grandes avancées, ne permettent cependant pas de décrire les interactions interspécifiques complexes. Il est pourtant crucial de comprendre à la fois comment les traits des organismes modulent les interactions biotiques, et comment ces traits et leur diversité influencent le fonctionnement des écosystèmes. Les résultats de cette thèse permettent de discuter la pertinence de ces différentes approches pour décrire la structure des communautés et leur rôle dans les processus écosystémiques.

6.2.2.1. Résolution taxonomique

Nous avons vu que se placer à différents niveaux de résolution taxonomique permettait de décrire différentes réponses de la macrofaune à son environnement. Plus précisément, la diversité des arbres semble augmenter la richesse, la diversité, et l'équitabilité de la macrofaune à une résolution taxonomique large (ordre) mais cet effet ne retrouve pas à un niveau de résolution plus fin (espèce). Ajuster le niveau de résolution taxonomique, ou « suffisance taxonomique » (Ellis 1985), est une méthode classiquement utilisée pour répondre aux objectifs d'une étude tout en minimisant le temps nécessaire à l'identification des organismes collectés. En s'intéressant aux patrons de diversité en fonction de différents gradient environnementaux, plusieurs études ont montré in réponse similaire au niveau spécifique qu'au niveau du genre chez les fourmis (Pik et al. 1999; Souza et al. 2016), de la famille et du groupe trophique chez les nématodes (Bhusal et al. 2014) et du genre et de la famille pour les acariens oribatides (Meehan et al. 2019). Dans notre cas, en adoptant un niveau de résolution taxonomique plus grossier nous avons également pu inclure davantage de taxon qu'à l'échelle spécifique. De cette façon, nous n'observons pas les mêmes réponses entre les différents niveaux de résolution. Cela suggère que la transposition des résultats d'un niveau de résolution à un autre n'est pas nécessairement automatique (Kaspari 2001), mais permet de décrire différentes relations intéressantes entre les organismes et leur environnement. La généralité de ces résultats doit être testée sur plus de groupes taxonomiques et dans des contextes environnementaux variés, ce qui pourrait se faire assez aisément à partir des études ayant déjà fait le travail d'identification à l'espèce.

6.2.2.2. L'utilisation des traits fonctionnels

Par un travail méticuleux de mesures individuelles et de recherche bibliographique, la description de la structure fonctionnelle des communautés de Carabidae a permis de décrire les mécanismes d'assemblage de leurs communautés. L'utilisation des traits pour la description des communautés des arthropodes terrestres, notamment du sol gagne en popularité. Afin d'assurer le bon développement de ce domaine et son pouvoir prédictif, des synthèses de littérature ont déjà travaillé à identifier les limites des études actuelles (Brousseau et al. 2018b; Wong et al. 2019). Ces synthèses insistent notamment sur l'importance d'utiliser des traits dont la relation avec des facteurs environnementaux ou des

processus écosystémiques sont documentés, et permettent de tester les hypothèses de l'étude. Plusieurs considérations méthodologiques sont également à prendre en compte, notamment sur la technique d'échantillonnage qui pourrait sélectionner certaines valeurs de traits, ou le protocole de mesure de traits morphologique qui doit être standardisé (Moretti et al. 2017). De nouvelles méthodologies se développent pour faire grandir les base de données de traits, et si nous sommes encore loin de l'ampleur de la base de donnée TRY (Kattge and Str 2020), l'action COST AUDAPHOBASE (CA18237 - European Soil-Biology Data Warehouse for Soil Protection) a pour objectif de réunir l'ensemble des bases de données existantes pour uniformiser l'information et faciliter encore l'utilisation de cette approche. Il est également encourageant de voir l'émergence de nouvelles approches tel que le projet ECOTAXONOMY (Sandmann et al. 2019) qui permet l'intégration des morpho-espèces et le renseignement de traits à différents niveau de résolution taxonomique. Ce système permet à la fois d'intégrer l'ensemble des individus collectés et non seulement ceux identifiés à l'espèce, mais également d'inférer les valeurs de traits manquantes à partir des traits d'un organisme phylogénétiquement proche. Enfin, le développement des analyses automatisées d'images par *machine learning* permettront dans un futur proche d'accélérer l'identification et la mesure de traits morphologiques et promettent ainsi d'améliorer notre pouvoir prédictif en élevant le nombre d'échantillons possible d'inclure dans nos études.

6.2.3 Interactions litière-macrofaune sapro-géophage

Etudier le comportement alimentaire de la macrofaune est important pour comprendre comment les espèces se partagent la ressource disponible, et la façon dont cette partition de ressource participe localement à la structuration spatiale, à la composition taxonomique et à la diversité des communautés écologiques. Dans nos résultats, une plus grande qualité de la litière favorise la diversité de la macrofaune sapro-géophage, tandis que la masse des horizons organiques est négativement corrélée à l'abondance et biomasse de ces organismes (chapitre 1). De plus, la qualité physico-chimique des litières semble moins importante que la morphologie des feuilles pour expliquer leur consommation par six espèces de macroarthropodes saprophages (chapitre 3). Ces résultats suggèrent que des propriétés des litières autres que leur qualité chimique doivent être considérées pour mieux expliquer l'influence de cette ressource sur la structuration des communautés de macrofaune. Plus

précisément, les propriétés reliées à la quantité et à la diversité des microhabitats semblent prometteuses (Hansen and Coleman 1998). Par exemple, les caractéristiques des microhabitats disponibles dans le bois mort (i.e. nombre et profondeur des fissures, densité du bois) ont été reliées à d'importants changements de composition des communautés de macrofaune, et la diversité de ces caractéristiques augmente le nombre de famille de macrofaune susceptibles de s'établir dans le milieu (Zuo et al. 2014, 2016). A ce jour, les études manquent pour distinguer l'effet relatif de la qualité de la ressource et de la provision de microhabitat car ces deux paramètres sont difficiles à dissocier sans une manipulation directe. Toutefois de nouveaux cadres conceptuels sont développés en ce sens (Dias et al. 2017). Fujii et al. (2020) proposent ainsi de réunir deux axes de variation des traits de la litière: 1) les traits reliés au « Plant Economic Spectrum (PES)» tels que la quantité d'azote et 2) ceux reliés au « Size and Shape Spectrum (SSS)» tels que la taille et la forme (Figure 5.1). Les premiers déterminent la qualité de la litière alors que les seconds sont reliés aux microhabitats que les feuilles peuvent représenter pour la faune. De plus, les auteurs intègrent ces deux axes dans l'espace et le temps, et montrent comment les valeurs des feuilles d'une espèce d'arbre varient sur l'axe PES et SSS au court du temps et de la stratification vertical de l'humus. Ce cadre conceptuel est prometteur, mais si les traits relatifs au PES sont désormais connus disponibles pour un grand nombre d'espèces de plantes (base de donnée TRY; Kattge et al., 2020) un grand effort sera également nécessaire pour définir et quantifier les traits morphologiques pertinents des litières reliés aux caractéristiques de microhabitat. Différents traits ont été proposés dans ce sens, notamment la tridimensionnalité et la courbure (Makkonen et al. 2012), qui renseigne sur la contribution de chaque feuille sur la disponibilité en microhabitat à l'échelle de la couche de litière. Dans cette thèse, nous proposons une mesure de la tubularité décrivant dans quelle mesure les feuilles s'enroulent sur elles-mêmes et qui décrit davantage les microhabitats à l'échelle de la feuille. Il sera également important à l'avenir de déterminer dans quelle mesure ces microhabitats sont effectivement utilisés par la faune, et par quels organismes. Dans notre cas, il était très fréquent sur le terrain d'observer des araignées ayant tissé leur toile dans les feuilles enroulées de l'arbousier, montrant que les prédateurs autant que les détritivores peuvent utiliser ces microhabitats, suggérant un rôle important de ces microhabitats pour les interactions proie-prédateurs. Plusieurs études ont d'ailleurs montré que le nombre d'interactions proie-prédateurs dépend de la disponibilité en

refuge pour les proies (présence de litière, Vucic-Pestic et al. 2010), de la quantité de litière qui peut réduire la probabilité de rencontre (dilution des populations de proie, (Kalinkat et al. 2013), ainsi que de la morphologie des feuilles (SLA, Santonja et al. 2018).

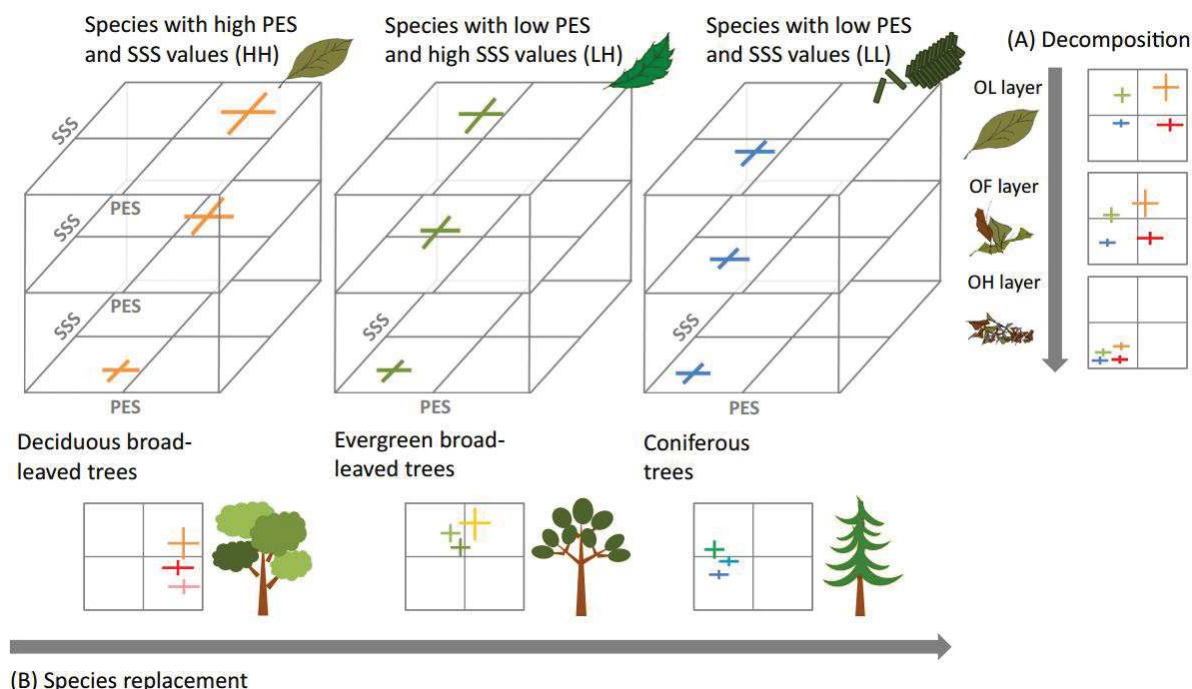


Figure 5.1 – Changement des traits des litières sur les axes PES et SSS, dans les différentes strates de l’horizon organique au cours de la décomposition, en présence de différents types de végétation. Chaque espèce de litière (3 différentes couleurs) occupe un certain volume fonctionnel dans l’espace défini par les traits liés au PES et SSS. L’évolution du volume occupé et déterminé par les changements de qualité (PES) et la fragmentation/décomposition des feuilles (SSS) et est représenté par la longueur des barres. Les valeurs des PES et SSS de l’horizon OL retournent à ses valeurs initiales à chaque nouvelle chute de litière. Extrait de Fuji et al. (2020).

6.2.4. Rôles de la macrofaune dans le fonctionnement du sol

Avec deux expérimentations à différentes échelles, et en incluant un nombre conséquent de 12 espèces communes en Europe (mis à part *Scherotheca gigas* dont la distribution est restreinte au sud de la France), les résultats obtenus permettent d’améliorer nos connaissances sur les conséquences de l’activité de la macrofaune sapro-géophage sur la transformation de la matière organique et les communautés de nématodes.

6.2.4.1. Transformation de la matière organique

L'expérience de préférence alimentaire du chapitre 3 montre qu'à partir d'un mélange homogène de litière de quatre espèces d'arbres, cinq des six espèces de macroarthropodes saprophages étudiées présentent des préférences alimentaires différentes et produisent des boulettes fécales aux propriétés physiques et chimiques différentes. Il en résulte à la fois un mélange de litière à la qualité moyenne différente que sans la faune puisque les proportions relatives de chaque espèce sont modifiées par la consommation sélective par les animaux, mais aussi la production d'un pool de matière organique à la qualité variable, qui ne dépend pas nécessairement de la composition de l'alimentation des animaux. La diminution globale des ratios C/N et C/P et de la teneur en tannins dans les boulettes fécales suggère un effet positif sur les communautés microbiennes (Swift et al. 1979; David 2014a). De plus, la capacité de rétention d'eau accrue des boulettes pourrait accentuer cet effet positif puisqu'il est démontré que la quantité d'eau de la matière organique influence fortement sa décomposition (Makkonen et al. 2012). Bien que non présentée dans cette thèse, la même expérience de préférence alimentaire a été réalisée avec les six espèces de vers de terre utilisées dans l'expérimentation à l'Ecotron (chapitre 4). Les résultats obtenus montrent que les vers endogés ne consomment pas les litières en surface, tandis que les anéciques le font, mais montrent des préférences pour certaines espèces de litière et des taux d'enfouissement variables d'une espèce à l'autre. L'épi-anécique *L. terrestris* est capable d'enfouir 12% de la litière, en sélectionnant principalement celle d'*A. monspessulanum* et de *Q. ilex*, tandis que *A. nocturna* n'en enfouit que 5% de la litière de quatre espèces mais principalement de *Q. ilex*, et que *S. gigas* n'en enfouit que 3% principalement d'*A. monspessulanum*. Les déjections des vers seront prochainement analysées afin de mieux caractériser leurs effets sur la transformation de la matière organique ingérée. Au-delà des transformations physico-chimiques que subit la litière lors sa digestion, il est crucial de quantifier sa redistribution dans les différents horizons du sol puisque celle-ci influence largement sa décomposition (Coulis et al. 2016a), et conditionne la distribution de la ressource et des microhabitats pour les microorganismes et la faune du sol (Decaëns et al. 1999; Erktan et al. 2020)

6.2.4.2. Diversité fonctionnelle

L'expérimentation en mésocosmes a permis et montrer, en plus des effets important des vers de terre endogés et des mille-pattes, qu'une plus grande diversité fonctionnelle de la macrofaune sapro-géophage avait tendance à favoriser la résistance de la structure du micro réseau trophique à des sécheresses prolongées. L'expérimentation est encore en cours et les futures données acquises (PLFA, perte en masse de litière) promettent de lever encore davantage le voile sur les multiples rôles que la macrofaune joue dans la décomposition, la structuration du sol, la composition et activité des microorganismes et nématodes, et les processus écosystémiques associés. A ce jour, il est saisissant de constater à quel point le nombre d'études s'intéressant à l'importance de la diversité fonctionnelle des plantes est élevé en comparaison de celui des travaux portant sur les organismes du sol et leurs effets sur le fonctionnement des écosystèmes. La poignée d'étude démontrant l'importance de la diversité fonctionnelle de la macrofaune du sol pour le fonctionnement des écosystèmes ne couvrent qu'un nombre limité d'espèces dans des conditions expérimentales souvent peu réalistes (Heemsbergen 2004; Hedde et al. 2010; Coulis et al. 2015a; Lubbers et al. 2020). De plus, les traits et les indices de diversité fonctionnelle utilisés diffèrent d'une étude à l'autre, limitant de fait la portée des comparaisons entre les résultats obtenus. Ce manque de connaissance est d'autant plus inquiétant si l'on considère que, appliquée aux communautés végétales, l'approche basée sur les traits fonctionnels n'est en mesure d'expliquer qu'une partie limitée des processus écosystémiques. Dans une récente étude sur les communautés végétales expérimentales en prairie, van der Plas et al. (2020) montrent que le pourcentage de variance des processus écosystémiques expliqué par les traits fonctionnels reste bas, autour de 13%, même en incluant 40 traits dans les analyses (Figure 5.2). Cette difficulté à prédire les fonctions écosystémiques à partir des traits provient probablement du besoin d'intégrer la phénologie des espèces puisque l'expression des traits dépend grandement du stade de développement de l'individu (Volaire et al. 2020).

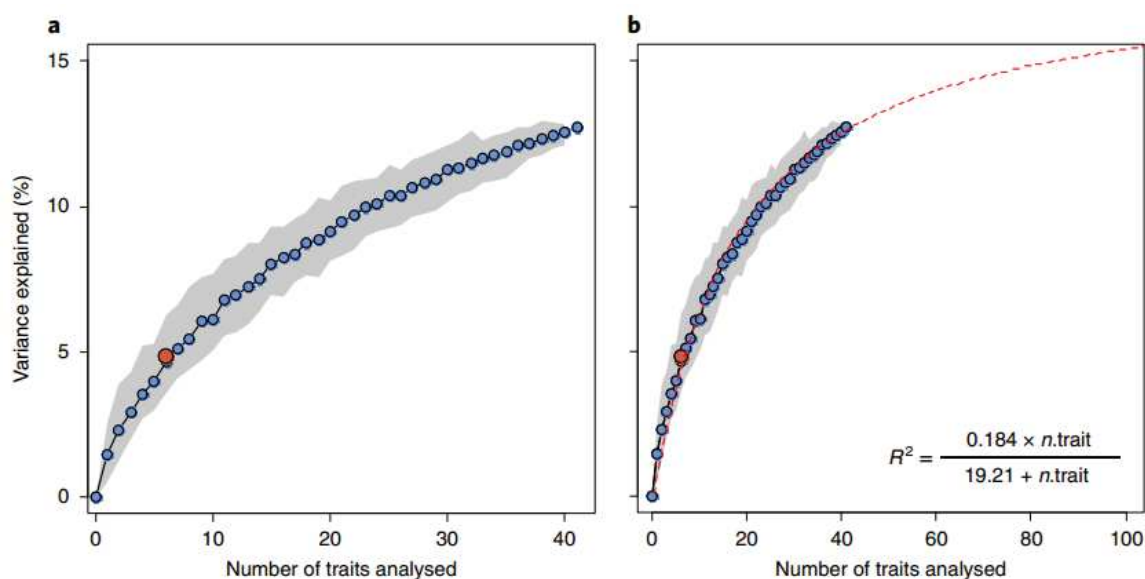


Figure 5.2 – Proportion de variance des processus écosystémiques expliquée en fonction du nombre de trait considéré dans une méta-analyse d'étude des communautés végétales prairiales (van der Plas et al. 2020) **a** à partir des données réelles et **b** extrapolation de Michaelis-Menten. Le point rouge représente la proportion de variance expliquée si seulement les six traits les plus classiquement utilisés sont intégrés.

L'application de l'approche basée sur les traits à la faune du sol requière l'inclusion de traits décrivant le comportement des organismes, mais ces traits sont difficiles à identifier et encore plus à quantifier. Décrire précisément dans quelle mesure les organismes du sol affectent la structure et porosité du sol par leurs déplacements dans les différents horizons semble être une voie prometteuse. En effet, en réponse à une méta-analyse montrant que la présence de vers augmente l'émission de gaz à effet de serre (GES), nous avons réalisé une expérience en microcosme en présence ou absence de plantes et simulant deux cycles de séchage-réhumidification (SR), laissant varier l'humidité du sol à la fois en fonction du traitement SR et de l'activité des vers. Nos résultats montrent que la présence de vers n'induit pas d'augmentation des émissions de GES, voire les réduit, notamment par l'augmentation du volume de macropores dans les horizons plus profonds (20-30cm), qui diminue le nombre de sites anaérobiques propices à la production de N_2O (Ganault et al. submitted). Les systèmes de galeries des vers de terre sont de mieux en mieux connus, notamment grâce aux analyses par tomographie au rayon X (Capowiez et al. 2015). En revanche, le rôle d'autres organismes du sol sur la création de galeries reste bien moins documenté et doit être davantage quantifié, compte tenu du fait que l'enfouissement est un comportement répandu pour survivre à la sécheresse, notamment chez les macroarthropodes saprophages (David and Handa 2010).

6.2.5. Sensibilisation du grand public

Dans les prochaines décennies, la science aura pour rôle de comprendre comment préserver la biodiversité des sols et les fonctions qu'elle assure, et ce dans un contexte de changement global opérant à de multiples échelles et entraînant des changements marqués dans la distribution des espèces et une altération profonde du fonctionnement, de la résistance, et la résilience des écosystèmes. Dans ce contexte, la science doit également tenir son rôle de transmission des savoirs, afin de faire grandir les prises de conscience sur les enjeux relatifs à la sauvegarde de la biodiversité et de changer les perceptions du grand public qui sont souvent négatives vis-à-vis des insectes et autres invertébrés (Leandro and Jay-Robert 2019). De nombreuses initiatives grandissent dans ce sens avec les Fêtes de la Sciences, les tribunes publiées par des ensembles de chercheurs dans des journaux grand public, la vulgarisation par l'art (voir l'illustration de cette thèse en bande dessinée en annexe 1), ou encore le développement de journaux scientifiques à destination des publics plus jeunes tels que *Frontiers for Young Minds* (voir mes deux contributions à une édition spéciale de ce journal sur la biodiversité des sols en annexes 1 et 2). Enfin, le développement de projets de sciences participatives semble également être un moyen prometteur pour à la fois sensibiliser le grand public tout en faisant progresser nos connaissances sur la biodiversité en générale (Cooper 2016). De nombreux projets sur la biodiversité du sol naissent (Auclerc et al. 2019), des outils utilisables par le grand public répondant aux exigences de rigueur scientifique se développent et promettent d'excitantes découvertes dans un avenir proche.

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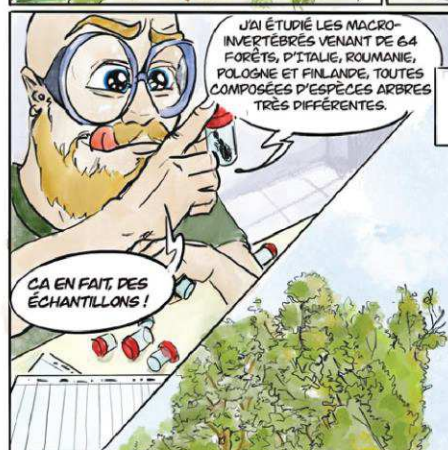
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Annexes



INDÉPENDamment DU PAYS D'ORIGINE, LES POPULATIONS DE MACRO-INVERTEBRÉS NE SONT PAS LES MÊMES SELON LE TYPE ET LA DIVERSITÉ D'ARBRES

PRENEZ UNE FORÊT D'ARBRES À FEUILLAGE CADUC, LA LITIÈRE (LES FEUILLES MORTES) EST DE TRÈS BONNE QUALITÉ NUTRITIVE : AU TOP POUR LES VERS DE TERRE !!



À L'OPPOSÉ, DANS UNE FORÊT D'ARBRES À FEUILLAGE PERSISTANT, LA LITIÈRE (LES FEUILLES MORTES) EST CONSTITUÉE D'AIGUILLE TRÈS LENTES À SE DÉCOMPOSER, ET PEU APÉTANTES POUR LES VERS DE TERRE.



En forêt mixte, c'est le parfait mélange ! La qualité de la litière satisfait les vers de terre, et est assez épaisse pour abriter les prédateurs. Une plus grande diversité d'arbres accueille donc une plus grande diversité de macro-invertébrés.

EN REVANCHE, LES PRÉDATEURS EUX, Y TROUVENT DE NOMBREUX HABITATS ET Y PROSPÈRENT.



How soil organisms look like reveals their role in the soil

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Abstract

There is a multitude of life forms on our planet. This is especially true under our feet, in the soil. Earthworms, spiders, and millipedes are only a few examples of the vast number of soil organisms. Once you look what lives in soils, you realize the tremendous diversity of shapes and colors. But what if we take the time to describe all their characteristics: color, size, shape, number of legs, type of wing, lifespan and climate preferences? All these characteristics, called traits, help us to understand what type of organisms can be found in a particular ecosystem, what they feed on, and how far they can go. Scientists use this information to understand the different roles of soil organisms in soils, and restore degraded soils. Doing so, they reveal how important soil organisms are, and why they play fundamental roles for human societies.

Keywords : earthworms, springtails, ground beetles, identification, morphological characteristics, soil processes

1658 words, 3 figures, 6 references.

Soil organisms' diversity: a wonderful but poorly known world

Under our feet, millions of organisms live in the soil (Orgiazzi et al. 2016). These organisms span from microscopic living forms (called micro-organisms) to more than one-meter long invertebrate organisms (such as earthworms that do not have vertebra). The variety of organisms in the soil is called soil biodiversity. Biodiversity designates the variations in all the life forms on the planet.

Soil ecologists are scientists who quantify the diversity of soil organisms. They usually travel (in a tropical rainforest or an agricultural field) and sample the soil organisms living there. They use shovels, traps, or corer to take out soil samples, depending on whether the organisms of interest live in the soil or on its surface (Fig. 1). Then, they catch by hand or with pliers the organisms they can see. Soil ecologists use different techniques to catch the smallest soil invertebrates. For example, at the laboratory, they place the soil sample in a funnel, below a

heating lamp and above a jar. The light and heat make the tiny organisms to go down, through the funnel into the jar. After a few days, scientist can collect them (Berlese method).

When all the soil organisms are collected, the long and meticulous part starts. Soil scientists count and observe very closely each individual organism to determine which species it belongs to (identification process). To do so, they use stereo-microscopes and microscopes, and identification keys and books. We then get the number of species present in one particular ecosystem, which is one of the most used index to quantify biodiversity. Soil scientists have a lot of work to do because soils are among the most diverse and highly human-impacted ecosystems on Earth. In addition, many soils in the world have not been studied yet, so that many species of soil organisms have not even been discovered yet.

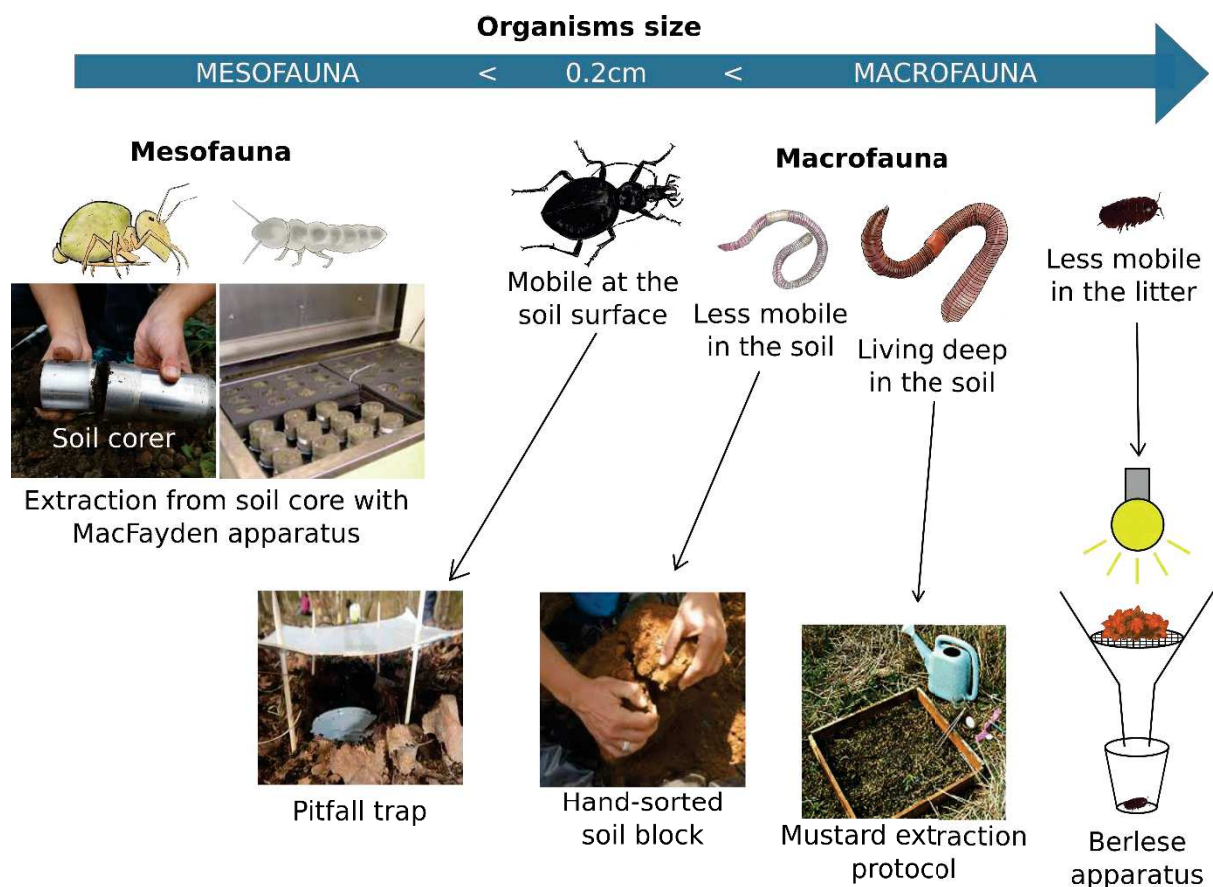


Figure 1 – Method to sample and study soil invertebrates' diversity. Small organisms (mesofauna) are extracted from a small soil core by drying it in the MacFayden apparatus and collecting individuals falling below. Large fast moving organisms (predators) living in the litter are collected when they fall in pitfall traps. Less mobile organisms living in the soil are extracted from a soil block with a shovel that is sorted by hands. Earthworms living deep in the soil are extracted by pouring mustard solution in their burrows. Less mobile organisms living in the litter (woodlice) are put in a Berlese apparatus that dries the litter and bring the organisms down in a jar, as the MacFayden apparatus. Drawing credits: www.lesbullesdemo.fr. Pictures credits: Apolline Auclerc, EcoBioDiv lab.

Grasping soil organisms' diversity by looking at their morphological characteristics (traits)

Soil biodiversity is so large that it is almost impossible to describe all soil organisms at once. Here, we will show the diversity of shapes and behaviors of soil organisms using three examples of well-studied groups (Fig. 2): earthworms, collembola (springtails) and a group of insects, the ground beetles (carabids).

Body size

The first morphological difference between those groups and between species within these groups is their body size. This is an example of a morphological trait. The smallest earthworm measures several centimeters while the largest, found in tropical forests, can be 2 meters long. In Europe, ground beetles measure between 2 mm and 8 cm from the top of their head to the last segment of their abdomen. Springtails are much smaller with an average body size of only 2 mm, but their size vary as well depending on where they live. Some species living in the trees' dead leaves (litter) are bigger than other small-bodied springtails which live deeper in the soil that is compacted.

Moving techniques

To find a habitat that offers high quantity of food, a place to reproduce with congeners, and a low number of predators, soil organisms have developed numerous techniques to move at the surface and into the soil. Earthworms do not have legs, but some species have strong muscles and small silks (sort of hairs) that they use to burrow and hang on the soil particles. With their 6 legs like all the insects, ground beetles can run at the soil surface to catch their preys. Many carabids' species have wings allowing them to rapidly escape from a predator or from a disturbance (e.g. ploughing), or to move to a place where they can find more preys or congeners. Springtails move also thanks to their 6 legs but also thanks to a special ventrally appendage, called furca, to escape predators. The furca acts like a spring: it is retracted against the body and when it deploys, the springtail jumps several dozens of centimeters in the air! **Only springtails living on the top of the soil have a furca, since it is not possible to jump in the soil.**

Colors of the body

Soil organisms can also be colorful. Some earthworm called 'epigeic' are fully reddish-brown, which enables them to camouflage from their predators inside the orange-brown dead leaves, but also to be UV-protected (**Bottinelli et al. 2020b**). They are adapted to live in the few first centimeters of soil, in the dead leaves, compost or manure. Other earthworms, named 'endogeic', live into the soil and are not pigmented with often pale colors (pale pink, grey or green). In this black box, pigmentation is not necessary because the UV does not go through soil. Other earthworms, called 'anecic', mostly live into the soil but they put their head out of the soil to feed on dead leaves; consequently, only their head is pigmented. Springtails show almost the same color patterns as earthworms: pigmented species live on top of the soil

(epiedaphic) and unpigmented ones live in the soil (euedaphic; Potapov et al. 2016). Finally, ground beetles can show many wonderful coloring patterns, especially those of the *Carabus* genus (such as *Carabus rutilans*). The vivid colors might discourage their bird predators, or might help them to camouflage in their environment.

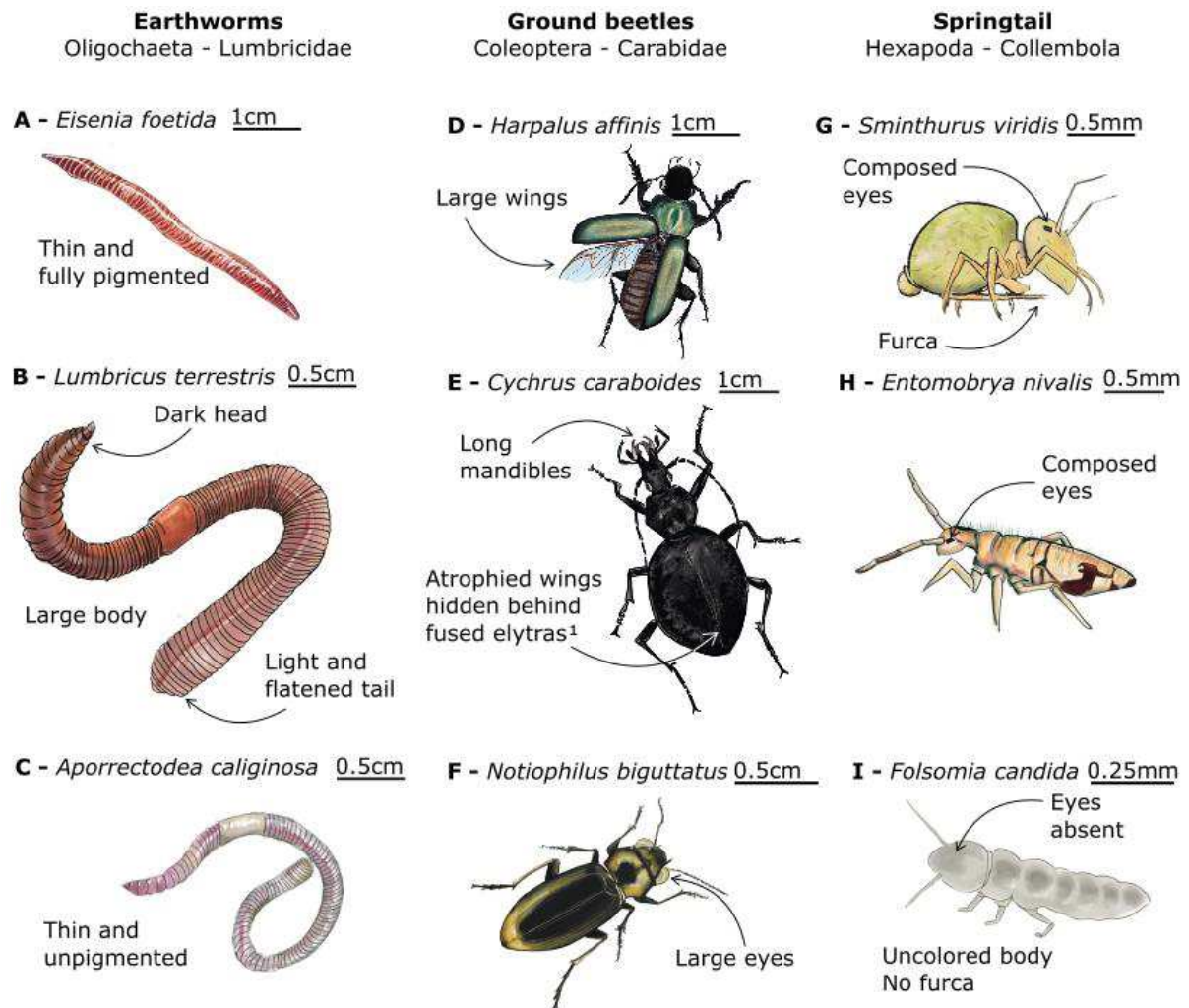


Figure 2 – Difference in morphological characteristics (traits) between 9 species of soil invertebrates belonging to three groups: earthworms, ground beetles and springtails. Drawings credits: www.lesbullesdemo.fr. ¹elytras are transformed wings protecting the animal as a shield (as the red part with black dots of the ladybug).

Mouth types

Another stinking difference between our three groups is their mouth type. Ground beetles have strong mandibles that can have different shapes and sizes depending on what they eat the most. For example, species of the *Cychrus* genus have very long mandibles, projected forward them, to reach inside the shells of snails. By eating fungi developing on dead leaves with their small mouth, springtails eat small pieces of leaves in between its veins, creating beautiful

skeletonized dead leaves. Earthworms do not have mandibles but their muscular stomach that is strong enough to crush the soil and the leaves they eat.

Guessing the role of soil organisms in the ecosystem from their morphological and behavioral characteristics (traits)

Meticulous observations of soil organisms' traits inform on what the organisms eat, where they live, and how they interact with their environment (Fig. 3), such as by changing the physical organization of soil by creating burrows, or by adding nutrients for plants to the soil thanks to the dead leaves transformation, or by controlling other organisms populations by eating them (Pey et al. 2014c).

First, earthworms play crucial roles in maintaining healthy soils by their intense burrowing activity. The endogeic and anecic earthworms live in the soil, and by moving through, eating and mixing the soil particles with pieces of dead leaves, they create a lot of burrows and dejections (named casts). In this labyrinth of burrows, air and water can circulate more easily (Capowiez et al. 2015), helping other soil organisms to drink and breathe, and plant roots to grow. Anecic earthworms are usually large organisms and create long and wide vertical burrows (very much like chimneys). Endogeic earthworms make a lot more thinner burrows than anecic ones, but still contribute strongly to soil aeration. Earthworms therefore are very important to reduce flooding, soil erosion, and improve soil health. Studying some morphological and behavioral features of earthworms, highly helps us to understand their role in the ecosystem.

Springtails also play crucial roles in soils, especially by their action in recycling nutrients from dead leaves for plant growth. In some cases, springtails can be very abundant and reach densities of 10-100,000 individuals per square meter! They can eat very large amount of litter and microorganisms (fungi and bacteria). After eating, they produce many small fecal pellets composed of very tiny pieces of dead leaves, mixed with some water present in their digestive tube. Fecal pellets are the perfect meal for microorganisms that will continue to transform dead leaves into nutrients that the plants can use. Recycling actions by springtails and microorganisms are very important for ecosystems and plant growth. Considering collembola species characteristics such as where they live (*e.g.* soil surface or into the soil), their preferred habitat (some species prefer meadows than forests), what and how much they eat, and their population densities, helps scientists to quantify their role in a given ecosystem.

Ground beetles generally are predators and can feed on a wide range of preys, from small aphids to larger snails. Certain species of ground beetles are specialized for the preys that they eat; for instance, the species *Cychrus caraboides* only feeds on snails. Some ground beetles catch tiny springtails thanks to their well-developed eyes, as the species of the genus *Notiophilus*. Carabids are important in regulating other animal populations, as in crops by feeding on the pests that would damage the plants. Farmers can therefore use ground beetles instead of chemicals to fight against pests. This is called biological control, because it uses natural interactions between organisms (predator-prey relations). It is important to maintain a high diversity of ground beetles in a given ecosystem because not all species will feed on the

same preys. Moreover, carabids vary in body size, and mostly eat preys that are smaller than themselves. Therefore, hosting a high diversity of predator species allows a higher regulation of pests (Rusch et al. 2015).

The body size, the mouthpart type and size, the hunting strategy, the type of preys (size and quantity) are important features that scientists consider to better understand the relationship between a soil invertebrate and their environment.

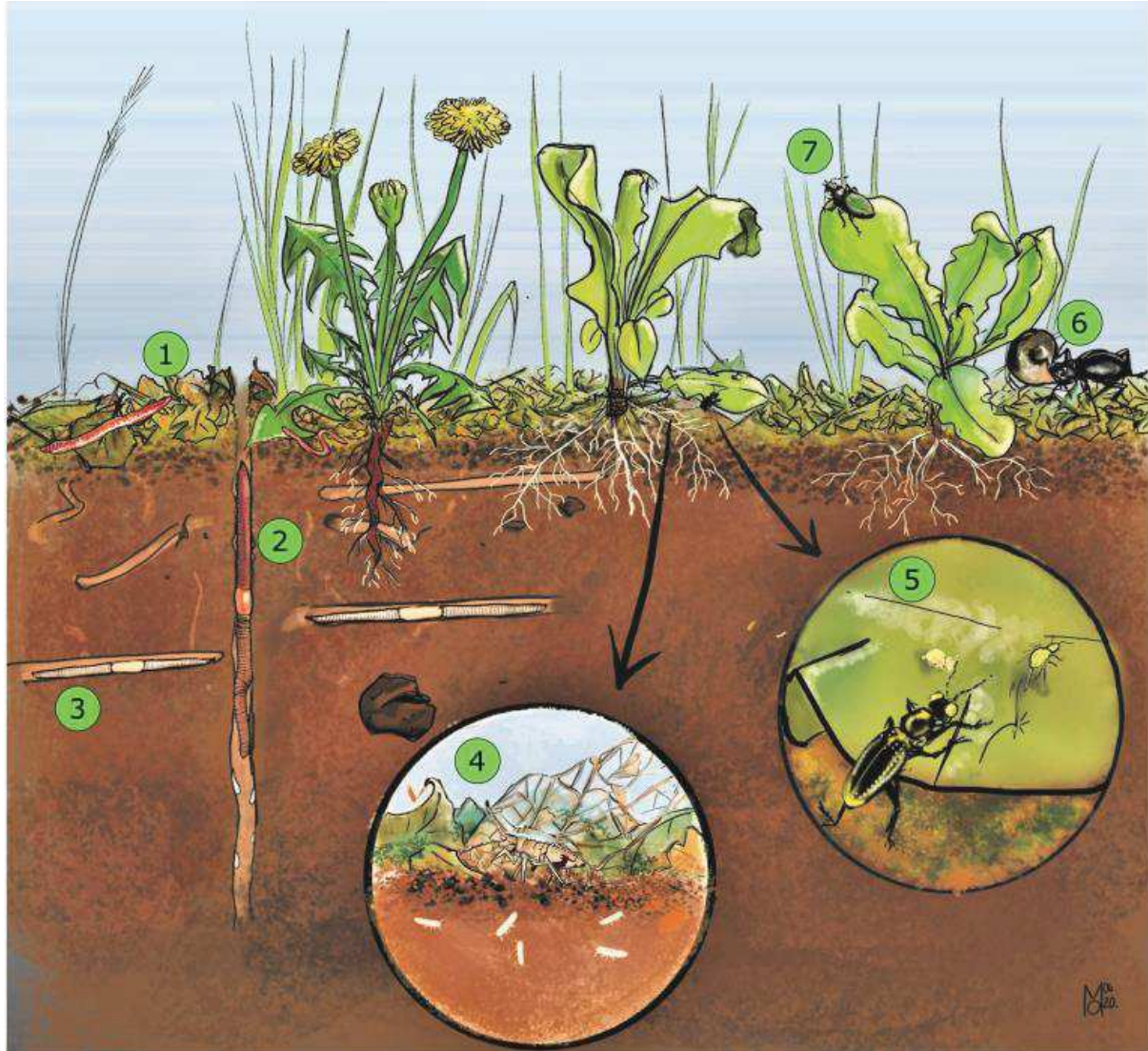


Figure 3 – Soil organisms in action. 1) Earthworm living and feeding on dead leaves (Epigeic, *Eisenia fetida*); 2) Earthworm reaching soil surface through its large and deep burrow (Anecic, *Lumbricus terrestris*); 3) Earthworms living into the soil and digging many burrows (Endogeic *Aporrectodea caliginosa*); 4) Different springtail species transforming dead leaves into fecal pellets (*Folsomia candida*, small white) and (*Entomobrya nivalis*, larger and yellow); 5) Springtail *Sminthurus viridis* escaping from the specialized predator *Notiophilus biguttatus*, by jumping with its furca; 6) Carabid (*Cychrus caraboides*) feeding on a snail; 7) Carabid ready to fly (*Harpalus affinis*). Drawings credits: www.lesbullesdemo.fr.

Conclusion

Soil organisms are incredibly diverse in shapes and behaviors. Soil ecologists have the chance to discover new species, and new characteristics to explore a wonderful world. By looking at species characteristics, soil scientists are able to better understand the interactions between organisms and ecosystems. All together the numerous roles played by soil biodiversity are complementary and fundamental to maintain healthy soils. It is thus very important to maintain and conserve soil biodiversity that is increasingly facing the impacts of human activities (such as intensive agriculture, or climate change). Raising public awareness and improving our knowledge on soil biodiversity will be key to decreasing our impacts on this amazing component of biodiversity.

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Glossary

Species richness: the number of species in a sample independently of how abundant are the species.

UV light: part of the sun's rays that are invisible to the naked eye and can cause sunburn.

Insects: organisms with exactly six legs and two pair of wings, some hardened called “elytras”.

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Earthworms and their role in greenhouse gas emissions

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Abstract

The living biomass of all earthworms is greater than the mass of any other animal species. Earthworms are involved in many soil processes, making them really important organisms to study. We first focus on earthworm diversity and ecology, how they feed and how they move through the soil. The consequences of earthworm activity for soil processes and inhabitants are then developed with a special focus on microbial communities and greenhouse gas (GHG) emissions. Indeed, in simplified laboratory experiments, earthworms promote microbial activity, leading to higher CO₂ and N₂O emissions by 33 and 42%, respectively. We detail the scientific methods to study the links between earthworm and GHG production from lab experiment to in-natura studies. Further we discuss important environmental factors such as soil texture and pH, the presence of plant or of drying-rewetting cycles. Earthworms' effects on soil processes are very complex and therefore scientifically challenging, important and exciting.

Keywords: climate change, land use, crops, experiment

1542 words, 3 figures, 6 references

Contribution to the field

Earthworms are a major component of soil biodiversity and their activity profoundly drives soil processes. Their role in stimulating microorganisms is of primary importance for nutrient cycling and plant growth, but may also affect greenhouse gas emissions. Our study exposes the role of earthworms for the mitigation of GHG emissions and the limits of human knowledge at this subject. Those links are especially important to understand considering the ongoing climate change and urge to adopt land use systems in urban and agricultural areas that both preserve biodiversity and limit global warming.

Earthworm diversity and ecology

Under our feet, thousands of animals live in the soil, notably the famous earthworms. 'Earthworms' actually refers to many species. Scientists described around 7,000 species worldwide, but some areas are poorly studied and scientists expect that there are more than 30,000 species that still need to be described [1]. Earthworms don't have bones (they are invertebrates), an external skeleton (contrary to insects), or even eyes, but they have strong muscles. They are able to move through the soil, and even eat it, along with some dead leaves. They don't differ a lot in their morphology and show contrasting lifestyles which can roughly be gathered into three main groups called 'ecological categories' [Fig. 1; ,2].

The first group, called "epigeics" (pronounced "ep-i-jEE-ik") are small earthworms (3-10 cm) with red-pigmented color, like the famous redworm *Eisenia fetida* commonly used in vermicomposting. They live in dead leaves and their color both protects them from UV radiation, and is a camouflage to hide from surface predators. Without digging into the soil, they eat dead leaves and transform them into small pieces of organic matter in their feces (casts). "Endogeic" (pronounced "en-d-oh-jEE-ik") earthworms are larger (5-15 cm) and completely unpigmented. They only live in the mineral soil and create numerous burrows (Fig. 1). In an experimental pot, 4 individuals of the *Aporrectodea caliginosa* species dug 2.2 km of burrows of 3.5 mm width per m³ of soil in only 6 weeks [3]! By digging their way, they also eat a lot of very little pieces of dead leaves that are in the soil, and mix organic matter with mineral soil (Fig. 2). The third group is "anecic" earthworms (pronounced "an-e-c-ik"), they are the largest (> 10 cm but up to one meter!). They dig few and deep vertical burrows (Fig. 1), like *Lumbricus terrestris*, that can dig burrows exceeding 1 meter in depth. During the night, they stick their head out to grasp dead leaves on the surface and bring them to deeper soil layers. Since almost only their head leaves the soil, only their head is pigmented.

Eating or burying dead leaves and moving through the soil by creating burrows are the two main actions of earthworms in soils. This has positive consequences on many soil properties, ecosystem processes and a great influence on other soil organisms, which earned earthworms the name of "ecosystem engineer".

Earthworm action in the soil and impact on microbial communities

Earthworm burrows profoundly change soil structure by creating large spaces in an environment otherwise more compact. Many organisms live in or close to burrows that are important habitat for small invertebrates, microorganisms such as bacteria, and plant roots. Burrows act also as pipes that increase water and oxygen fluxes to deeper soil layers. This effect on water and gas fluxes depends on earthworm ecological categories. In the same experiment of Capowiez et al. (2015), done in PVC tube (16cm diameter, 30cm height), the

endogeic *A. caliginosa*' burrows allowed a water infiltration rate of 5.2 L per minute, while this rate increased to 12.4 L per minute in the anecic *L. terrestris*' burrows.

In ecosystems where earthworms live and are abundant, dead leaves don't accumulate on the soil surface and disappear quite quickly during their season of activity. Epigeic earthworms transform dead leaves to smaller pieces in their casts, and anecic earthworms bury dead leaves in deeper soil layers. Endogeic earthworms then eat small dead leaves or root particles with mineral soil and excrete it behind them wherever they go. Combined, this results in the vertical and horizontal redistribution of organic matter: instead of an accumulation at soil surface, this resource is more homogeneously available for living roots and other soil inhabitants.

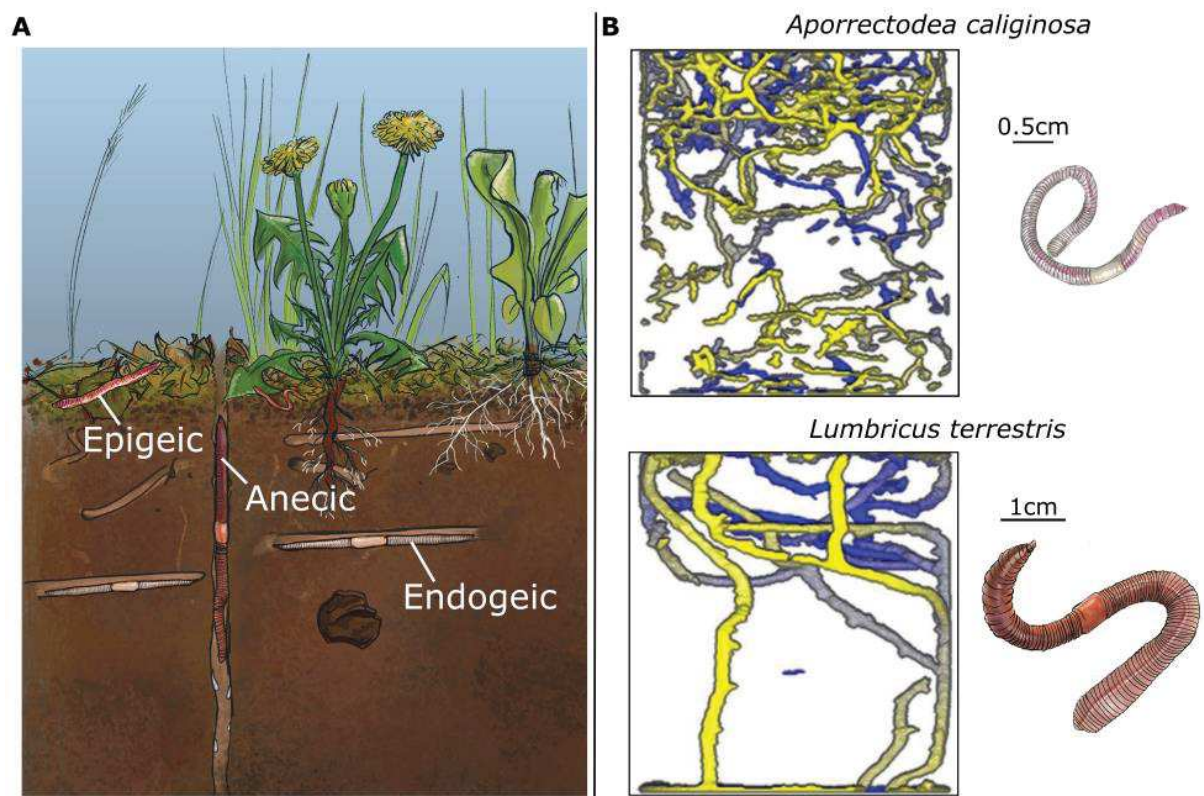


Figure 1 – The three main earthworm ecological categories (A) and X-ray 3D reconstruction of the burrow systems (B) of one endogeic species (*Aporrectodea caliginosa*) and one anecic species (*Lumbricus terrestris*), in experimental plots (PVC tube of 16 cm diameter, 30 cm height); colors are given for 3D rendering (yellow in the foreground and blue in the background); taken from Capowiez et al. (2015). Drawings credits www.lesbullesdemo.fr

All these modifications markedly affect other important and famous actors in soils: bacteria. These microorganisms need the right balance of food, water and air to live. They will transform the small pieces of organic matter into even smaller particles, notably of carbon and nitrogen. These particles are so small that plant roots can now absorb and use them to grow. When

growing and breathing, bacteria use food composed of carbon, water, and oxygen (O_2) and produce carbon dioxide (CO_2). If there is too much water, as during a flood or in rice fields, they can't breathe anymore. In this case, they use food made of nitrogen and water, and produce dinitrogen (N_2), and nitrous oxide (N_2O). CO_2 and N_2O are important greenhouse gases (GHG), meaning that these gases increase the atmosphere's temperature, driving the ongoing climate change.

In soils, bacteria may lack either organic matter, air, or water, and be less active. Earthworms may wake up bacteria by modifying organic matter, water and air availability. Scientists observed that this effect is even stronger in earthworm's gut (Fig. 2), since like humans, earthworms have bacteria living in their intestines. Indeed, in the gut, organic matter and mineral soil are perfectly mixed, in an environment saturated with water. This is a transient heaven for bacteria that produce N_2O [4]. By stimulating bacteria that produce CO_2 and N_2O , we can therefore wonder if earthworms will increase or decrease GHG emissions.

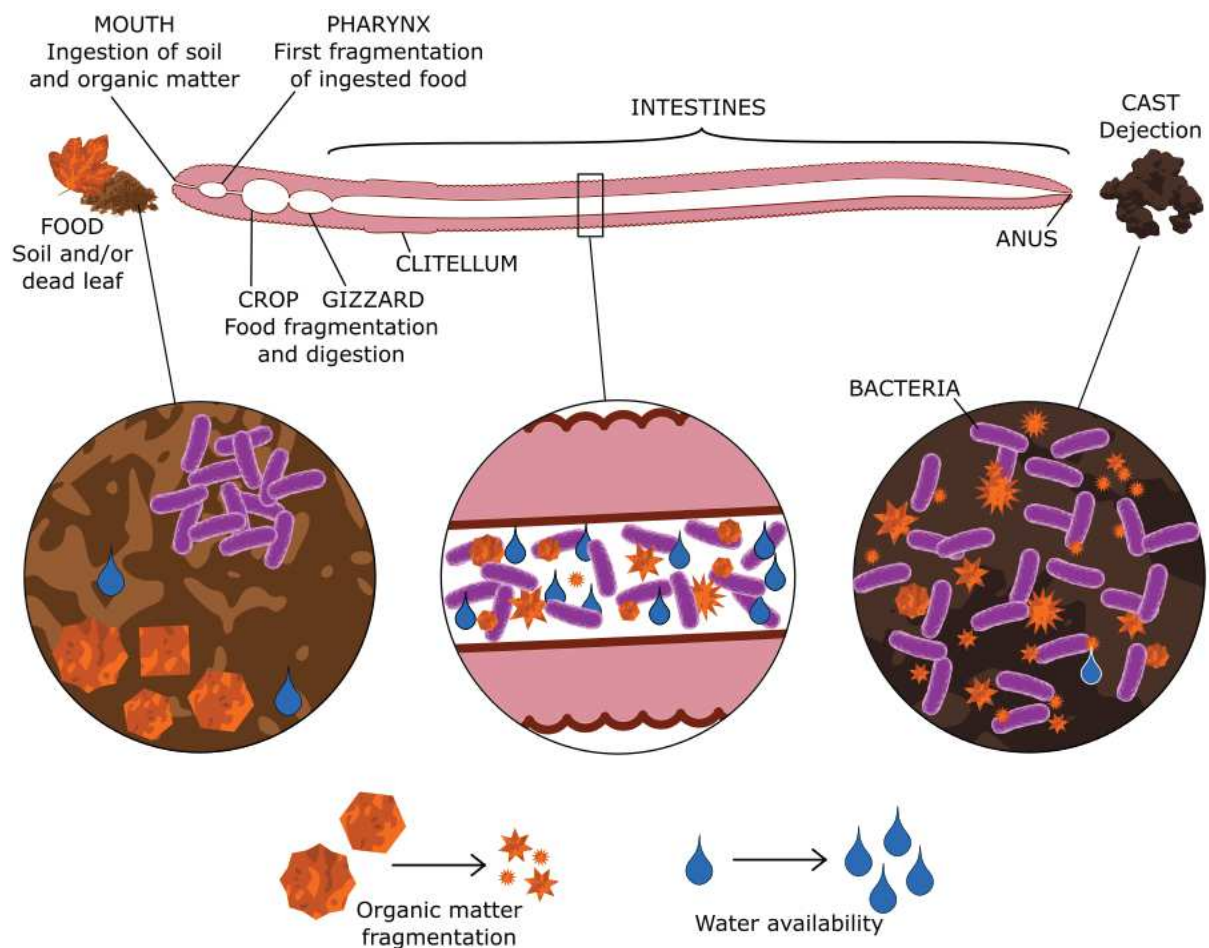


Figure 2 – Consequences of passing through the earthworm digestive track for organic matter, water availability and microbial communities. Inspired from Drake & Horn, 2007.

Methods and their limits to study earthworm impacts on GHG emissions

One way to study earthworm effects on bacteria activity and GHG emissions is to run laboratory experiments. To do so, we use pots of different size, usually small to easily manipulate them. We fill the pots with soil, after sieving it to remove rocks, other animals and roots. Then we add earthworms, usually a few individuals of the same earthworm species, ideally in number close to natural abundances. We keep some pots without earthworms as a control. Then we measure GHG emissions at the soil surface and study bacterial communities in pots with or without earthworms, and see where the emissions are higher.

Another method is to directly measure gas production in natural ecosystems. In this case, we gently push cylinders (chambers) into the ground, where gases (CO_2 and N_2O) will accumulate and can be measured (Fig. 3). Then we sample earthworms in the soil and try to relate GHG emissions to the abundance or diversity of earthworms present. It is also possible to measure other important variables for bacteria activity: soil water content, organic matter availability, pH...

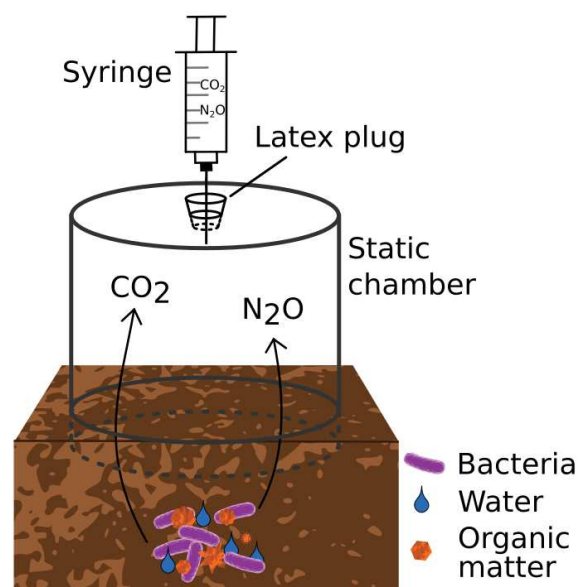


Figure 3 – Design of a static chamber used to measure GHG emissions. Gases produced by bacteria accumulate in the sealed static chamber, and then are sampled with a syringe through the latex plug.

A last tool is to gather all the existing studies and look across all the resulting data if GHG emissions are higher or lower in presence of earthworms. Compiling 57 studies, it was found that on average, earthworms increase CO_2 emissions by 33% and N_2O emissions by 42% [5]. This would mean that, although being highly beneficial for soil health and fertility, earthworms may have in return a detrimental effect on GHG emissions because they increase bacteria activity.

This seems like a real dilemma: earthworms improve soil fertility, and at the same time increase GHG emissions? However, important experimental limits reduce our understanding of earthworms' role in GHG emissions. GHG emissions originate from the very complex interactions between earthworms, microbes, soil properties, plants, and water availability. These factors are very difficult to manipulate in experiments, and very variable in the field.

Limits to our understanding

The first important factor is the great diversity of soil properties, such as sand content. Earthworms generally prefer soils with a low content of sand because these soils dry faster and sand particles can be abrasive for their skin. Soil pH can also strongly affect earthworms that may not survive in too acidic soil (below pH=4.5). It would be inefficient to make experimental pots for the thousands of different soil types, and our knowledge is currently limited to certain common soil types.

Secondly, very few studies included plants in the experiments. Plants absorb water and nutrients with their roots, reducing their availability for earthworms and bacteria. However, plants and bacteria also help each other. Plant roots produce sugar in the surrounding soil that bacteria can eat in exchange of minerals that these bacteria were able to absorb a little further from the roots. Unfortunately, it is really difficult to experimentally test all these simultaneous positive and negative interactions.

Thirdly, the vast majority of studies kept the soil's water content constant. This is generally done to optimize earthworm activity. However, doing so will overestimate negative earthworm effects. Indeed, in nature, soil are submitted to drying-rewetting cycles that depend on rainfall, vegetation cover, and soil structure, and earthworms can be completely inactive if the soil gets too dry. In a lab experiment imposing such drying-rewetting cycles, the presence of earthworms actually reduced N₂O emissions [6]. The authors of the study reasoned that earthworm burrows increased water fluxes to the bottom, and aerated the soil, which accelerated soil drying and reduced bacteria activity. Drying-rewetting cycle effects are really important to study as they are expected to be more frequent and extreme in the future.

Conclusion

Here we showed how complex GHG emissions from the soil can be. Earthworms modify organic matter distribution and water and air availability in soil which modify bacteria activity. However, bacteria also depend on soil physical properties, drying-rewetting cycles and plants. Much more work is needed if we want to manage our soil, notably in cropland, in a way that simultaneously sustains the highest diversity of soil organisms as earthworms without risking the promotion of GHG emissions.

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