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Associations plantes-sol le long de gradients environnementaux : des groupes trophiques aux multiples fonctions écosystémiques

Camille Martinez Almoyna

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THÈSE

Pour obtenir le grade de

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Spécialité : **BIODIVERSITÉ – ÉCOLOGIE - ENVIRONNEMENT**

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Présentée par

Camille MARTINEZ ALMOYNA

Thèse dirigée par **Wilfried THUILLER**, Directeur de recherche,
Laboratoire d'Écologie Alpine, et
codirigée par **Tamara MÜNKEMÜLLER**, Chargée de recherche,
Laboratoire d'Écologie Alpine

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dans l'**École Doctorale Chimie et Science du Vivant**

Associations plantes-sol le long de gradients environnementaux : des groupes trophiques aux multiples fonctions écosystémiques

Thèse soutenue publiquement le **jeudi 27 mai 2021**,
devant le jury composé de :

Wilfried THUILLER

Directeur de recherche, LECA UMR UGA CNRS, Directeur de thèse

Tamara MÜNKEMÜLLER

Chargée de recherche, LECA UMR UGA CNRS, Membre invité

Stephan HÄTTENSCHWILER

Directeur de recherche, CEFE CNRS, Rapporteur

Matthieu CHAUVAT

Professeur des universités, Université de Rouen, Rapporteur

Francesco FICETOLA

Professeur, Università degli Studi di Milano, Examinateur

Sandra LAVOREL

Directrice de recherche, LECA UMR UGA CNRS, Examinatrice

Jérôme POULENARD

Professeur des universités, Université Savoie Mont Blanc, EDYTEM,
Président



Biodiversité. Je cherche depuis des années comment expliquer pourquoi ce mot me fascine. Je cherche les mots pour décrire la beauté à la fois simple et complexe de la plus commune des pâquerettes. Ce mélange d'échelles et toutes ces différences avec l'Homme. L'unicité de chacun de ses traits, ce choix dans le hasard qui rend visible l'infini, parce qu'il s'est concrétisé, là, à nos pieds, dans cette association de formes, de couleurs, de mécanismes, dans cette espèce aussi insignifiante qu'une virgule, aussi merveilleusement agencée qu'une cathédrale. Il n'y a rien de nouveau, ni de sexy, dans cette petite pâquerette qui pousse dans le caniveau. Puissent les chercheurs et tous les curieux du monde s'asseoir sur le trottoir, puissent-ils stopper leur quotidien pour l'observer, cette biodiversité, pour s'en émerveiller. Puissent-ils encore avoir l'espace et le temps de se demander, mais comment cette pâquerette trouve-t-elle ici les nutriments nécessaires, mais pourquoi grandir là où l'Homme a bétonné toutes traces apparentes de vie ?

« Il y a deux réponses à ta question, comme à toutes les questions.
Celle du poète, et celle du savant.
Laquelle veux-tu en premier ? »

Ellana, P. Bottero

INTRODUCTION GENERALE.....	3
I. LES ACTIVITES BIOLOGIQUES DES PLANTES ET DE LA BIODIVERSITE DU SOL LES PLACENT PARMI LES ACTEURS PRINCIPAUX DES CYCLES BIOGEOCHIMIQUES.....	6
A. <i>Les plantes, au cœur du cycle du carbone et des nutriments</i>	6
B. <i>La biodiversité du sol, actrice principale de la décomposition</i>	8
C. <i>L'interdépendance entre plantes et sols, moteurs des cycles biogéochimiques</i>	10
D. <i>Vers une compréhension du fonctionnement macro-écologique des systèmes plantes-sol : que manque-t-il ?</i>	11
II. VERS UNE PRISE EN COMPTE DE L'ENVIRONNEMENT : UTILISATION DE GRADIENTS D'ALTITUDE POUR COMPRENDRE LA REPONSE DES PLANTES ET DE LA BIODIVERSITE DU SOL AUX CHANGEMENTS ENVIRONNEMENTAUX.....	15
A. <i>Les gradients d'altitude peuvent servir d'expérience naturelle pour comprendre la réponse des écosystèmes aux changements environnementaux</i>	15
B. <i>L'étude des liens entre environnement et plantes et biodiversité du sol présente un intérêt particulier dans les écosystèmes alpins</i>	16
C. <i>ORCHAMP – un observatoire spatio-temporel de la biodiversité et du fonctionnement des écosystèmes de montagne</i>	17
III. ADOPTER UNE APPROCHE MULTI-TROPHIQUE POUR PASSER DES ACTIVITES BIOLOGIQUES DES ORGANISMES A LA QUANTIFICATION DE LA CONTRIBUTION DES COMMUNAUTES DE PLANTES ET DU SOL AUX PROCESSUS BIOGEOCHIMIQUES.....	19
A. <i>Les plantes comme modèle d'étude historique des liens entre communautés et processus biogéochimiques</i>	19
B. <i>Limites et lacunes des approches appliquées aux communautés de plantes</i>	21
C. <i>Combiner échantillonnage des organismes du sol par métabarcoding, approche multi-trophique, et mesures de composition pour prendre en compte les communautés du sol</i>	22
1. <i>Le métabarcoding de l'ADN environnemental pour améliorer les connaissances taxonomiques dans le sol</i>	22
2. <i>L'approche multi-trophique des communautés : regrouper les espèces qui ont des rôles similaires dans la communauté pour pouvoir prendre en compte leurs interactions trophiques</i>	23
3. <i>Approcher la composition des groupes trophiques</i>	24
IV. VERS UNE APPROCHE SPATIALE DU FONCTIONNEMENT DES ECOSYSTEMES.....	26
A. <i>Le concept de fonctionnement de l'écosystème, intrinsèquement lié à l'Homme</i> ...	26
B. <i>... constitue un changement de perspective par rapport aux cycles biogéochimiques</i>	26
C. <i>... qui permet de modéliser plus facilement le fonctionnement des écosystèmes de façon spatialement explicite et en fonction de l'environnement</i>	27
V. PLAN DU MANUSCRIT.....	29
REFERENCES DE L'INTRODUCTION GENERALE.....	30
PRODUCTIONS ACADEMIQUES	37
SYNOPSIS DU PREMIER CHAPITRE.....	38

CHAPITRE 1, MULTI-TROPHIC B-DIVERSITY MEDIATES THE EFFECT OF ENVIRONMENTAL GRADIENTS ON THE TURNOVER OF MULTIPLE ECOSYSTEM FUNCTIONS.....	39
DU PREMIER CHAPITRE AU CHAPITRE 2 (ET AU RESTE DE LA THESE)	53
CHAPITRE 2, DIFFERENTIAL EFFECTS OF SOIL FOOD WEBS ON DECOMPOSITION IN MOUNTAIN ECOSYSTEMS.....	55
DU CHAPITRE 2 AU CHAPITRE 3	79
CHAPITRE 3, CLIMATE, SOIL RESOURCES AND MICROBIAL ACTIVITY SHAPE THE DISTRIBUTIONS OF MOUNTAIN PLANTS BASED ON THEIR FUNCTIONAL TRAITS.	81
DU CHAPITRE 3 AU CHAPITRE 4	94
CHAPITRE 4, STRONG LINKS BETWEEN PLANT TRAITS AND MICROBIAL ACTIVITIES BUT DIFFERENT ABIOTIC DRIVERS IN MOUNTAIN GRASSLANDS	95
DISCUSSION GENERALE.....	127
I. SYNTHESE DU TRAVAIL EFFECTUE POUR LA PRISE EN COMPTE DE LA VARIABILITE SPATIALE DES CONDITIONS ENVIRONNEMENTALES DANS LA MODELISATION DU LIEN ENVIRONNEMENT – BIODIVERSITE – FONCTIONNEMENT DES ECOSYSTEMES.	129
II. SYNTHESE DU TRAVAIL EFFECTUE POUR L’INTEGRATION DES INTERACTIONS ENTRE ESPECES DANS LA MODELISATION DU LIEN ENVIRONNEMENT – BIODIVERSITE – FONCTIONNEMENT DES ECOSYSTEMES.	131
III. SYNTHESE DU TRAVAIL EFFECTUE POUR LA MODELISATION DU FONCTIONNEMENT DES ECOSYSTEMES DANS SON ENSEMBLE.....	133
IV. PERSPECTIVES A COURT TERME : FUTURES PISTES DE PROGRESSION POUR LA RECHERCHE SUR LE LIEN ENTRE ENVIRONNEMENT, BIODIVERSITE ET FONCTIONNEMENT DES ECOSYSTEMES.....	134
A. <i>Améliorer la connaissance des prédicteurs environnementaux des différents groupes trophiques.</i>	135
B. <i>Prendre en compte les réseaux épigés.</i>	137
C. <i>Aller vers une modélisation multivariée de la multifonctionnalité</i>	140
REFERENCES DE LA DISCUSSION GENERALE	141
ANNEXES.....	145
1. ANNEXES DU CHAPITRE 1.....	146
2. ANNEXES DU CHAPITRE 2.....	160
3. ANNEXES DU CHAPITRE 3.....	176
4. ANNEXES DU CHAPITRE 4.....	186
RESUME.....	196
ABSTRACT	197
REMERCIEMENTS	198

Introduction générale



Au cœur des associations plantes-sol

Il est intéressant de constater que la naissance de l'écologie en tant que science indépendante coïncide avec l'expansion du capitalisme et avec la Révolution Industrielle. Lorsque le terme écologie est défini par Haeckel en 1866, la question des conséquences de l'exploitation de la nature se pose déjà, et taraude les philosophes et les artistes (Deléage, 1992). Alors qu'on est en train de résoudre une partie des mystères des 'cercles de la vie' (Dumas & Boussingault, 1844), par la suite appelés cycles biogéochimiques, certains comptent déjà les espèces qui ont disparu depuis l'apparition de l'Homme (de Tribolet, 1886). La découverte de l'équation de la photosynthèse est encore assez récente, on commence à entrevoir le rôle des microorganismes dans les cycles des éléments (de Saussure, 1804; Hellkriegel & Wilfarth, 1889; Winogradsky, 1890), et parallèlement on multiplie les recherches pour tenter de comprendre les rapports de l'Homme à la nature (Deléage, 1992; Geddes, 1884), notamment en questionnant la place de l'énergie dans le processus économique.

Ce lien important entre l'écologie et les conséquences des activités humaines a ensuite été perdu pendant presque un siècle, durant lequel l'écologie se développe surtout comme science naturelle. La plupart des connaissances et des concepts sur lesquels ma thèse s'appuie se développent à cette période : notamment, en 1927, le concept de chaîne alimentaire (trophique) est utilisé pour la première fois par Charles Elton. Il élargit également le concept de niche écologique¹ (Grinnel, 1928), pour y intégrer la place d'une espèce dans le réseau trophique (Elton, 1927). L'application de ce concept à différentes communautés permet (qualitativement) de dégager des généralités dans le fonctionnement des communautés animales, et de réintégrer les animaux dans les représentations des communautés vivantes, à l'époque encore souvent limitées aux plantes. Par la suite, Tansley introduit la notion d'écosystème, qu'il définit comme composé non seulement des organismes vivants mais aussi des facteurs physiques (Tansley, 1935). Il rapproche ainsi le système d'étude en écologie de la notion de système en physique. Par-là, il ouvre la porte aux travaux de Lindeman, qui applique les principes thermodynamiques aux écosystèmes. Lindeman mesure les flux d'énergie et de matière au sein d'un réseau très simplifié, où les nœuds représentent des grands groupes d'organismes vivants, et considère que ce réseau est l'écosystème (Lindeman, 1942). À la suite de Lindeman, un très grand nombre d'études mesurant les flux de matière et d'énergie au sein de réseaux simplifiés en un petit nombre de niveaux trophiques permettront de confirmer la place prépondérante des plantes, des décomposeurs, de leurs consommateurs et des prédateurs au sein des cycles biogéochimiques (Figure 1, Barnes *et al.*, 2018, 2014; Buzhdygan *et al.*, 2020; Odum, 1956; Schwarz *et al.*, 2017).

Plus d'un demi-siècle plus tard, la question des conséquences des activités humaines pour l'humanité est redevenue centrale en l'écologie (Cardinale *et al.*, 2012; Deléage, 1992; Vitousek, 1994). En effet, l'augmentation des concentrations de dioxyde de carbone dans l'atmosphère, due à l'utilisation des énergies fossiles, a engendré un réchauffement du climat, qui, selon certaines estimations, pourrait encore augmenter de plus de 4 °C avant la fin du siècle (IPCC, Collins *et al.*, 2013). Les changements d'utilisation des terres ont entraîné une érosion des sols telle qu'elle devient un problème majeur pour l'agriculture (IPCC, Shukla *et al.*, 2019). Enfin, les espèces vivantes disparaissent à un rythme sans précédent (IPBES, Díaz *et al.*, 2019).

¹ Place d'une espèce dans son environnement, contrainte et causée par des paramètres abiotiques (conditions environnementales) et biotiques (interactions avec les autres espèces).

Face à ces constats alarmants, une branche de l'écologie nommée Biodiversity Ecosystem Functioning émerge dans les années 1990, avec pour but de prédire les conséquences que pourraient avoir les disparitions d'espèces pour la survie de l'Homme (Loreau *et al.*, 2001). Il s'en suit une nette augmentation de l'utilisation du concept de fonctionnement des écosystèmes,

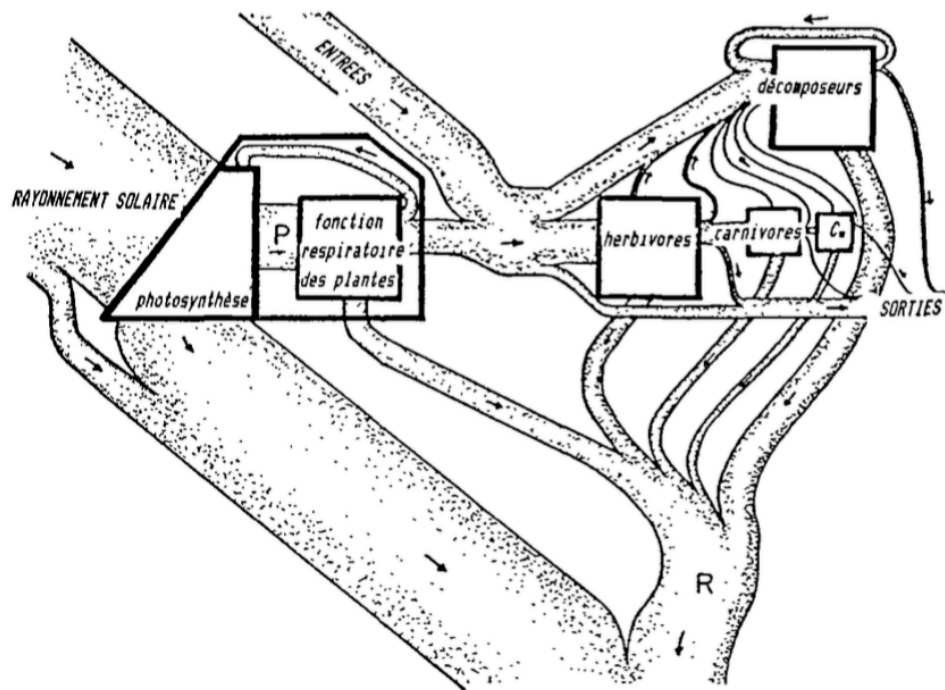


Figure 1 | Diagramme généralisé du flux d'énergie pour des communautés naturelles dans un état stationnaire, d'après Odum (1956). P est la productivité primaire brute, R est la respiration totale de la communauté. Cinq niveaux trophiques sont représentés par des quadrilatères de différentes tailles. Les flux qui partent du haut des carrés correspondent à l'énergie non-assimilée par les niveaux trophiques ; ceux qui partent du bas, à l'énergie utilisée pour la respiration. Le premier principe de la thermodynamique est illustré par l'égalité des flux entrant et sortant de chaque niveau trophique ; le second par les flux respiratoires qui accompagnent chaque processus et qui correspondent à la dissipation d'énergie sous forme de chaleur (Deléage, 1992).

qui, à partir de ce moment-là, désigne l'ensemble des propriétés des écosystèmes et des processus biologiques et biogéochimiques permettant d'évaluer l'état des écosystèmes dans un contexte de changement global (Jax, 2010; ESA, Naeem *et al.*, 1999).

Ma thèse s'inscrit dans cette lignée, entre écologie des organismes, des réseaux trophiques et des écosystèmes, et a pour but de faire un pas de plus vers la prédiction du fonctionnement des écosystèmes, notamment dans l'espace géographique. Pour atteindre cet objectif, je me concentrerai sur les plantes et la biodiversité du sol, car leurs activités biologiques sont au cœur des cycles biogéochimiques.

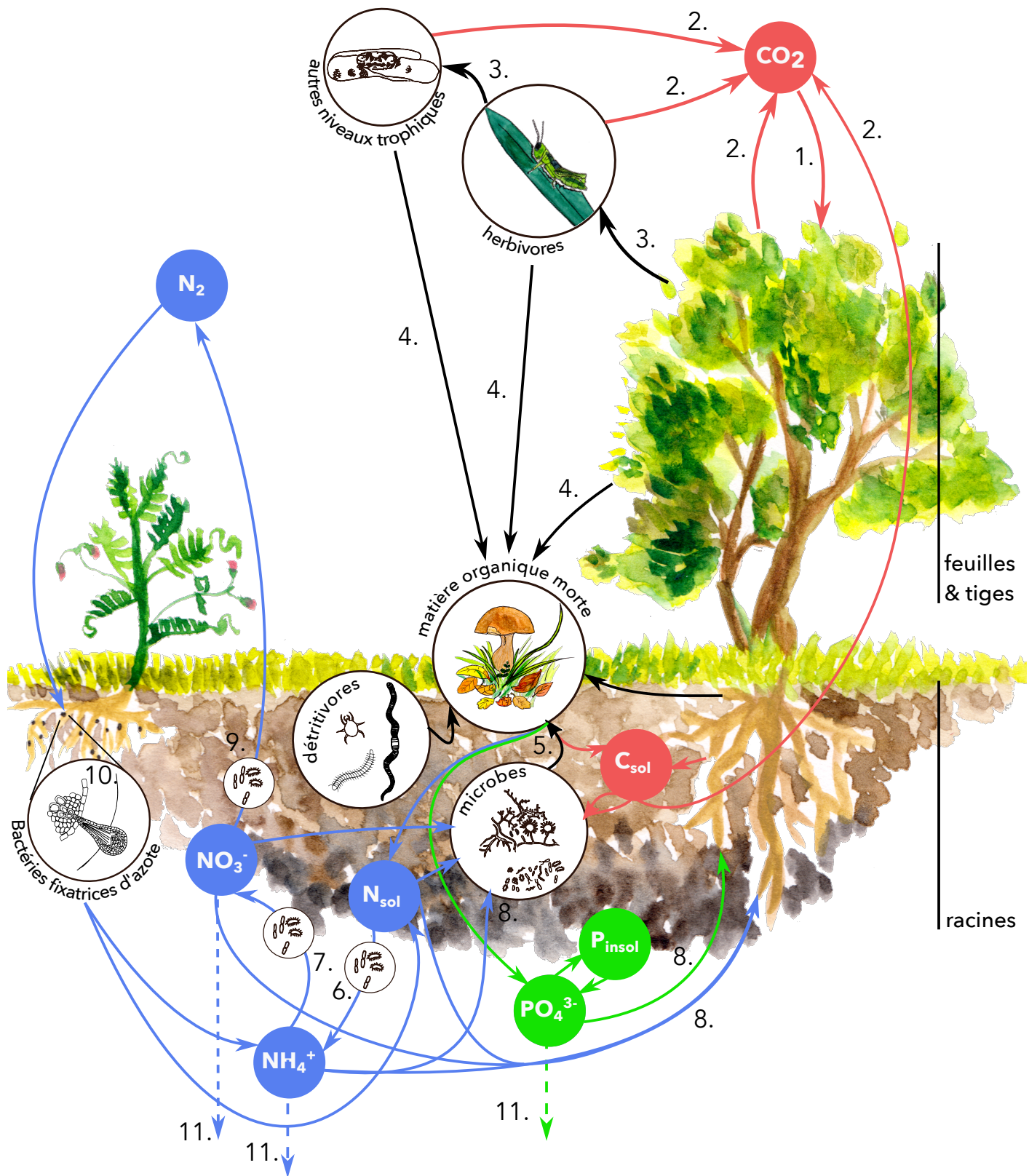
I. Les activités biologiques des plantes et de la biodiversité du sol les placent parmi les acteurs principaux des cycles biogéochimiques.

A. Les plantes, au cœur du cycle du carbone et des nutriments.

Les plantes, vivantes ou mortes, sont des acteurs fondamentaux des cycles du carbone et des nutriments (Austin & Zanne, 2015). Elles jouent tout d'abord un rôle clef dans le cycle du carbone en fixant le CO₂ atmosphérique, qu'elles transforment majoritairement en biomasse végétale grâce à la photosynthèse (Begon, Townsend, & Harper, 2006; Körner, 2003). Ainsi, les plantes sont des producteurs primaires, et constituent un des compartiments de base des réseaux trophiques (Figure 2, Wardle & Bardgett, 2002).

Cependant, l'influence d'une plante ne s'arrête pas lorsqu'elle meurt. Les débris de plantes constituent la majorité de la matière organique qui est progressivement désintégrée dans les sols, jusqu'au recyclage complet des éléments qui la constituent en CO₂, en eau et en nutriments inorganiques (décomposition, figure 2, Begon *et al.*, 2006; Hobbie, 2015; Wardle & Bardgett, 2002).

Figure 2 (à droite) | Les associations plantes-sol, au cœur des cycles biogéochimiques, inspirées de ressources.uved.fr. Les flèches et cercles rouges, bleus et verts représentent respectivement les réactions liées au cycle du carbone, de l'azote et du phosphore. Les différents cycles sont couplés au sein des organismes vivants, ce qui est représenté par les flèches noires. 1. Photosynthèse, les plantes fixent le CO₂ de l'atmosphère en sucres, ensuite utilisés pour le métabolisme ou pour construire la biomasse végétale, 2. Respiration, les plantes, les organismes du sol, les herbivores et les autres organismes des niveaux trophiques supérieurs dégradent les sucres en CO₂, ce qui libère l'énergie nécessaire à leur métabolisme, 3. Relation trophique, les organismes hétérotrophes se nourrissent de biomasse végétale ou animale et obtiennent ainsi les sucres et nutriments nécessaires à leur métabolisme et à la construction de leur propre biomasse, 4. Constitution de la litière, issue de la biomasse morte des plantes, microbes et animaux, 5. Décomposition, la matière organique morte des plantes, microbes et animaux est progressivement dégradée par les organismes du sol en composés organiques de plus en plus simples, d'abord insolubles (fragments) puis solubles, ou dissous, dans la solution du sol. 6 & 7. Respectivement, ammonification et nitrification, les molécules d'azote solubles (acides aminés par exemple) sont minéralisées. Plusieurs produits libérés par la minéralisation de l'azote et du phosphore dans le sol peuvent être réutilisés par les plantes et les microbes (8.). Certaines bactéries catalysent la dénitrification (9.), ce qui libère du diazote dans l'atmosphère. La fixation de l'azote de l'air (10.) dans le sol se fait par des orages ou par des bactéries en symbiose avec des plantes (ex. légumineuses). Enfin, les nutriments minéraux en excès dans le sol sont lessivés (11.) par les précipitations.



B. La biodiversité du sol, actrice principale de la décomposition.

Dans le sol, une immense diversité d'organismes participe aux cycles biogéochimiques.

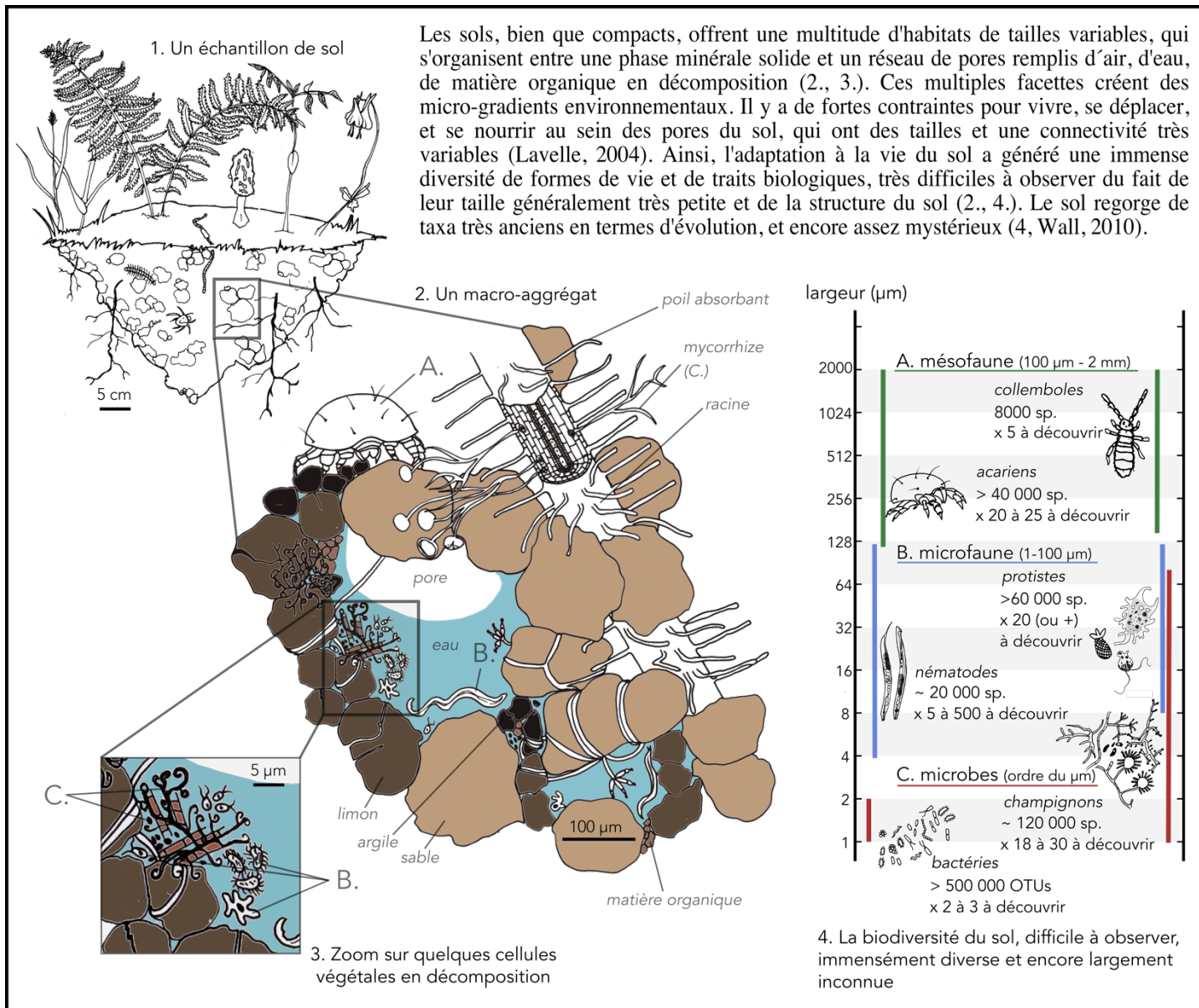
En premier lieu, les microbes (bactéries et champignons, Box 1) sont des acteurs primordiaux des cycles du carbone et de nutriments (Coleman, Callahan, & Crossley, 2018; Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Ritz, K., Six, J., Strong, D.R. & van der Putten, 2012; Wardle & Bardgett, 2002). Bien que fondamentalement différents - les bactéries ont besoin de la solution du sol pour vivre et se déplacer, tandis que les champignons forment souvent de grands hyphes qui leur permettent d'accéder plus facilement à la matière organique morte en surface - ces deux groupes colonisent la matière organique morte et participent à sa décomposition grâce à différentes enzymes qu'ils ont à leur surface ou relâchent dans le milieu (enzymes extracellulaires ou exoenzymes, Figure 2, Burns *et al.*, 2013). Les enzymes catalysent la succession de réactions nécessaires à la dégradation des débris organiques en molécules de plus en plus simples, jusqu'à atteindre des formes monomères (ex. carbohydrates² et protéines³ respectivement dégradés en sucres et acides aminés). Ces monomères peuvent être ensuite soit directement réutilisés, soit minéralisés, entre autres par les bactéries et champignons eux-mêmes (Figure 2). Les taux de décomposition, mais aussi les stocks de carbone, ainsi que le type et la quantité de nutriments disponibles dans le sol, dépendent donc de l'activité des bactéries et des champignons (Begon *et al.*, 2006).

De plus, les organismes du sol qui appartiennent à des classes de tailles plus grandes peuvent aussi influencer les cycles biogéochimiques via les réseaux trophiques. En d'autres termes, leur importance dépend de leur alimentation.

La microfaune, d'une part, module les cycles du carbone ou des nutriments indirectement, en régulant l'activité des microbes et la productivité des plantes desquels ils se nourrissent, ou via le rejet de nutriments dans leurs excréments (Begon *et al.*, 2006; Coleman *et al.*, 2018). Dans cette thèse, nous allons surtout nous intéresser aux protistes et aux nématodes. Les protistes, d'une part, sont des eucaryotes unicellulaires qui sont dépendant de la solution du sol pour pouvoir se déplacer (Box 1). Ils se nourrissent majoritairement de bactéries, mais certaines espèces ou groupes d'espèces consomment plutôt des champignons, et ils peuvent également être omnivores ou prédateurs (Adl *et al.*, 2019; Geisen, 2016). D'autre part, les nématodes sont des petits vers ronds qui vivent dans la solution du sol ou près des racines des plantes (Box 1). Ils ont un régime alimentaire plutôt spécialisé, que l'on reconnaît facilement grâce à la morphologie de leur bouche. Ils peuvent se nourrir uniquement de bactéries, de champignons ou de plantes, mais peuvent aussi être prédateurs ou omnivores (Coleman *et al.*, 2018; Nguyen *et al.*, 2016).

² Carbohydrates : molécules de matière organique riches en énergie et en carbone

³ Protéines : molécules issues de matière organique organiques riches en nutriments



Box 1 | Les organismes du sol dans leur milieu, inspiré de figures originales de K. Luoma, S. Rose et E.T. Elliott, respectivement dans Hartel (2004) et sur le site de la FAO (fao.org). Les richesses spécifiques des différents groupes taxonomiques, ainsi que les estimations du nombre d'espèces qui restent à découvrir sont issues des publications suivantes : collemboles, Thibaud & D'Haese, 2010 ; acariens, Walter & Proctor, 2013 ; protistes, Adl et al., 2007 ; nématodes, Poinar, 2012 ; champignons, Hawksworth & Lücking, 2017 ; bactéries, Louca, 2019.

La mésofaune, d'autre part, participe aux cycles biogéochimiques d'une manière assez similaire à la microfaune, comme acteur des réseaux trophiques du sol et en régulant les populations de microbes (Coleman *et al.*, 2018; Thakur & Geisen, 2019). Cependant, ils peuvent aussi avoir des rôles plus indirects. Par exemple, ils peuvent faciliter l'accès des bactéries et des champignons à la matière organique, soit parce qu'ils l'enfouissent et la redistribuent lorsqu'ils creusent pour se déplacer dans le sol, soit parce qu'ils déchiquent la matière organique en plus petits morceaux lorsqu'ils se nourrissent, soit parce que leur alimentation comprend à la fois de microbes et de débris de plantes (Figure 2, Box 1, Begon *et al.*, 2006; Thomas W. Crowther, Boddy, & Hefin Jones, 2012; Thakur & Geisen, 2019; Trap, Bonkowski, Plassard, Villenave, & Blanchart, 2016). En ce qui concerne la mésofaune, ma thèse est surtout restreinte aux acariens et aux collemboles (Box 1). On en trouve un grand nombre d'espèces aussi bien dans la litière en surface que plus profondément dans le sol, plus précisément dans les pores remplis d'air (Mitchell, Urpeth, Britton, Black, & Taylor, 2016; Potapov *et al.*, 2017). Les acariens ont des régimes assez variés et peu spécifiques. Ils peuvent être herbivores, bactériovores, fongivores ou prédateurs (Briones, 2014). Moins généralistes, les collemboles se nourrissent majoritairement de champignons et d'algues, mais on retrouve également très souvent des débris de plantes dans leurs intestins (Briones, 2014; Chahartaghi, Langel, Scheu, & Rues, 2005).

C. L'interdépendance entre plantes et sols, moteurs des cycles biogéochimiques.

Finalement, les cycles biogéochimiques, notamment du carbone et des nutriments, sont régulés par les interactions directes et indirectes entre les plantes et la biodiversité du sol (Figure 3).

Premièrement, les interactions directes entre plantes et biodiversité du sol forment un réseau de matière et d'énergie qui participe aux cycles biogéochimiques, notamment parce que le carbone et les nutriments y sont immobilisés sous forme de biomasse vivante, ou utilisés pour le métabolisme (Wardle *et al.*, 2004).

Parallèlement, les interactions indirectes entre plantes et organismes saprotrophes constituent une sorte de mutualisme indirect : les débris de plantes mortes apportent l'énergie et les nutriments sous forme organique aux organismes saprotrophes, qui décomposent cette matière organique puis la minéralise en formes inorganiques, à nouveau disponible pour les plantes. Cependant, la croissance des plantes et des organismes saprotrophes nécessitent toutes les deux de satisfaire certaines contraintes stœchiométriques, ce qui a une influence sur les cycles biogéochimiques. En effet, la production d'une unité de biomasse de plante ou d'organisme du sol nécessite des proportions de carbone, d'azote et de phosphore fixées par leur espèce. Cependant, les tissus des organismes du sol sont caractérisés par des proportions d'azote et de phosphore beaucoup plus importantes que celles des tissus des plantes. Les organismes du sol ont donc besoin de beaucoup plus de nutriments que les plantes pour produire leur propre biomasse, ce qui les met en compétition avec les plantes pour les nutriments inorganiques du sol. Il en résulte que, selon sa composition chimique, la matière organique issue d'une plante morte ne peut supporter qu'un certain nombre de microorganismes, et que le processus de

décomposition lui-même est limité par la disponibilité en nutriments (Begon *et al.*, 2006; Wardle *et al.*, 2004).

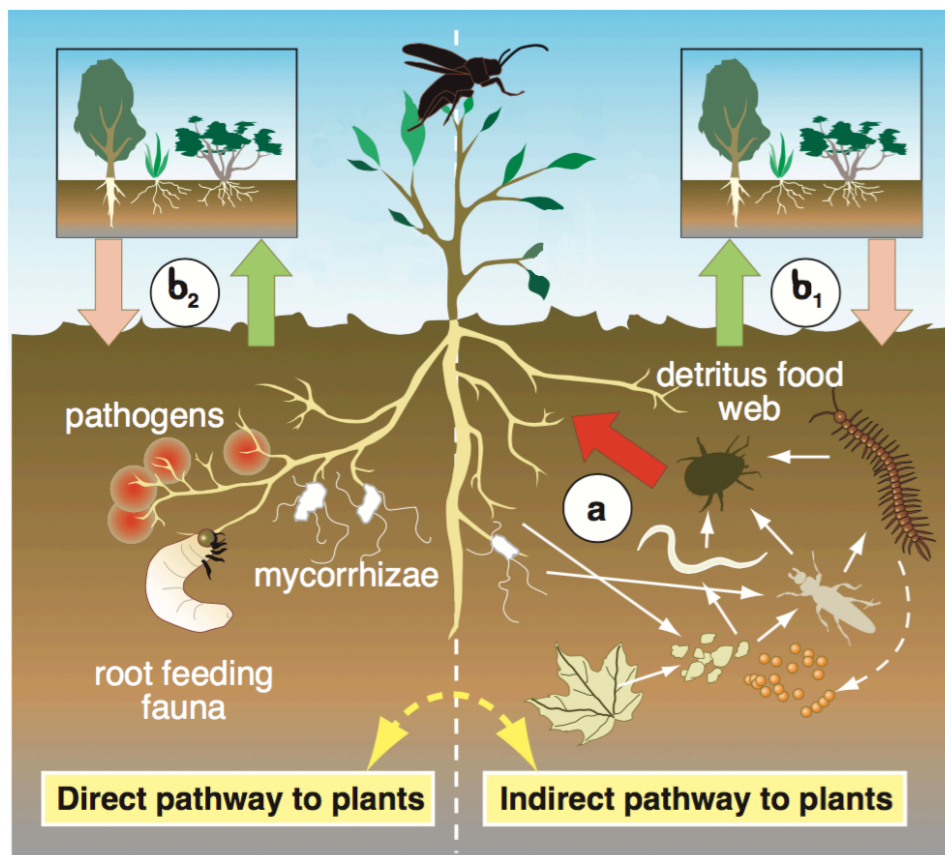


Figure 3 | Interactions entre les plantes et les organismes du sol, d'après Wardle *et al.* (2004). À gauche, les organismes du sol exercent des effets directs sur les plantes en se nourrissant des racines et en formant des relations antagonistes ou mutualistes avec leurs plantes hôtes. Sur la droite, les interactions trophiques du réseau détritique (flèches blanches) stimulent le recyclage des nutriments (flèche rouge épaisse), l'acquisition des nutriments par les plantes (a) et la performance des plantes. En outre, le réseau trophique du sol peut contrôler le développement successif des communautés végétales, à la fois directement (b2) et indirectement (b1), et ces changements dans les communautés végétales peuvent à leur tour influencer les organismes du sol.

D. Vers une compréhension du fonctionnement macro-écologique des systèmes plantes-sol : que manque-t-il ?

Théoriquement, on peut donc supposer qu'on a déjà une assez bonne idée des mécanismes individuels (processus) qui expliquent la place des plantes, de la biodiversité du sol et de leurs interactions directes et indirectes dans les cycles biogéochimiques. Cependant, la majorité de ces connaissances reste issue d'expériences contrôlées, ou réalisées à petite échelle, ce qui limite encore notre capacité à prédire et cartographier le fonctionnement des écosystèmes à large échelle.





Notamment, il est tout d'abord nécessaire de mieux comprendre comment les mécanismes présentés rapidement introduits précédemment dépendent de l'environnement (Brose & Hillebrand, 2016; Eisenhauer *et al.*, 2019; Gonzalez *et al.*, 2020). En effet, la plupart de ces

processus biogéochimiques sont directement influencés par le climat. Par exemple, la décomposition dépend d'une succession d'enzymes qui, par essence, présentent des optimums de température. De plus, les propriétés physico-chimiques du sol (ex. la disponibilité en nutriments inorganiques) dépendent du type de roche-mère sur laquelle le sol se forme, ce qui pourrait par exemple influencer les taux de décomposition (Körner, 2003). Enfin, et pour faire transition avec le deuxième point, climat et sol influencent également la biodiversité elle-même, en sélectionnant des plantes et des organismes du sol adaptés à un environnement particulier (Thuiller *et al.*, 2013). Le long de gradients environnementaux, les plantes et les organismes du sol ne sont pas assemblés aléatoirement, et on ne connaît pas les conséquences de la composition de ces assemblages sur les cycles biogéochimiques et a fortiori, sur le fonctionnement des écosystèmes (Box 2, Lavorel & Garnier, 2002; Lavorel *et al.*, 2013).

Deuxièmement, il est nécessaire de passer de l'échelle des organismes individuels à celle de la communauté (i.e. de l'assemblage d'espèces qui coexistent dans un environnement commun), et de mieux comprendre et quantifier les mécanismes qui lient localement la communauté de plantes et d'organismes du sol aux différents processus biogéochimiques dans lesquels elle est impliquée (Hines *et al.*, 2015; Loreau *et al.*, 2001). En effet, chaque espèce participe aux processus biogéochimiques différemment. Par exemple, la quantité de biomasse produite par chaque espèce de plante dépend de ses traits fonctionnels. A l'échelle de la communauté, la quantité de biomasse produite dépendra donc de l'assemblage des traits fonctionnels des différentes plantes (Box 2, Lavorel & Garnier, 2002). De plus, au sein d'une communauté locale, les espèces s'influencent via différents types d'interactions (ex. compétition, facilitation, interactions trophiques). Il en résulte que l'effet de deux espèces sur un processus biogéochimique n'est pas forcément additif (Hines *et al.*, 2015; Schleuning, Fründ, & García, 2015). Par exemple, il est possible qu'en présence de champignons saprophytes, certaines espèces de bactéries ne produisent pas d'enzymes pour décomposer la matière organique, alors même qu'elles en ont le potentiel génétique (Schneider *et al.*, 2010). Enfin, pour quantifier l'importance des différentes communautés de plantes et d'organismes du sol dans les cycles biogéochimiques, il faut donc pouvoir caractériser, décrire ces communautés (notamment en termes de diversité, de composition). Ceci n'est pas une tâche facile à large échelle (en particulier dans le cas des organismes du sol, T. W. Crowther *et al.*, 2019; Guerra *et al.*, 2020).

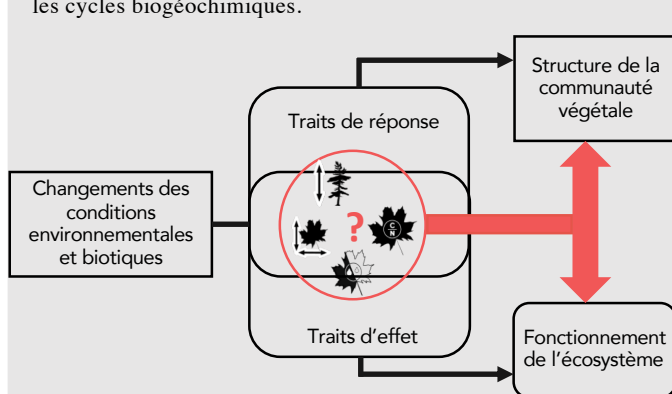
Box 2 (à droite) | Cadre conceptuel des traits fonctionnels et relation au fonctionnement de l'écosystème

Historiquement, le concept de **trait** remonte à Darwin, et était utilisé pour mesurer la performance d'un individu (Darwin, 1859). Parallèlement, les écologues ont très tôt groupé les espèces de plantes selon des caractéristiques morphologiques communes (ex. types de Raunkiaer). L'émergence de l'écologie fonctionnelle a associé les deux avec le concept des **traits fonctionnels**, qui désignent des caractéristiques morpho-physio-phénologiques impactant la performance des individus (Violle 2007). Les traits fonctionnels ont ensuite été utilisés pour quantifier les effets des espèces et des communautés de plantes sur les écosystèmes (1., Lavorel & Garnier, 2002), puis étendus à d'autres niveaux trophiques (3., Lavorel 2013, Gravel 2016). Quelques exemples de traits :

 <p>Hauteur végétative (plant height) = Distance la plus courte entre les tissus photosynthétiques et le sol, par ex. associé à la vigueur compétitive.</p>	 <p>Surface foliaire spécifique (SLA, specific leaf area) = Ratio de la surface d'un côté d'une feuille fraîche par sa masse sèche, par ex. associé au taux photosynthétique massique maximal</p>	 <p>C/N des feuilles (Leaf C/N) = Ratio des concentrations de carbone et d'azote totaux par unité de matière sèche de feuille, par ex. associé à la qualité nutritionnelle</p>	 <p>Quantité de matière sèche des feuilles (LDMC, leaf dry matter content) = Ratio de la masse sèche d'une feuille par sa masse fraîche, par ex. associé à la durée de vie de la feuille</p>
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1. Des traits de réponse et d'effet pour les communautés végétales (d'après Lavorel & Garnier, 2002)

Les **traits de réponse** caractérisent la réponse des plantes aux conditions environnementales (ex. disponibilité en ressources, perturbations) et déterminent donc la structure la communauté végétale. Les **traits d'effets** sont associés à l'effet des plantes sur les cycles biogéochimiques.

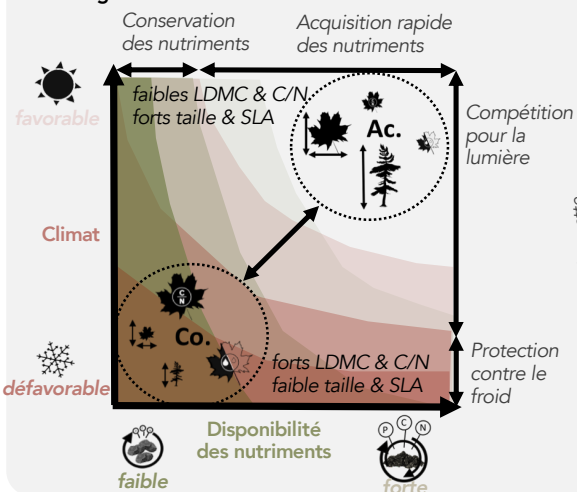


Ce cadre conceptuel permet d'articuler la réponse à l'environnement et les effets sur l'écosystème de la communauté de plantes via un certain degré de chevauchement entre les traits de réponse et d'effet de la communauté végétale (? rouge), qui dépend des variables environnementales.

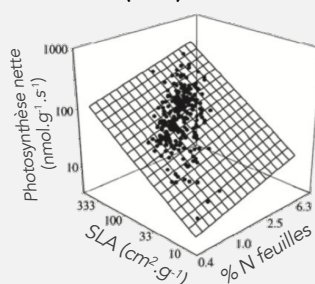
2. Théorie de l'économie des plantes (plant economics spectrum)

À l'échelle globale, on a montré qu'il y a un chevauchement fort entre les traits de réponse et d'effets liés à l'acquisition des ressources, à cause d'un compromis évolutif entre une stratégie conservative et lente (voir A., Co.) et une stratégie acquisitive et rapide (voir A., Ac., Reich 2014, Wright 2004).

A. Stratégies et liens entre traits en fonction du climat et du sol

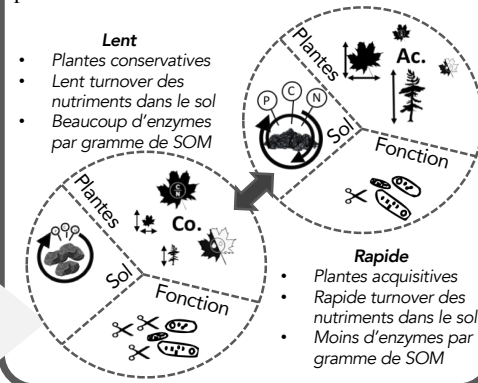


B. Conséquences des associations de traits sur le fonctionnement des écosystèmes, issu de Reich (2012)



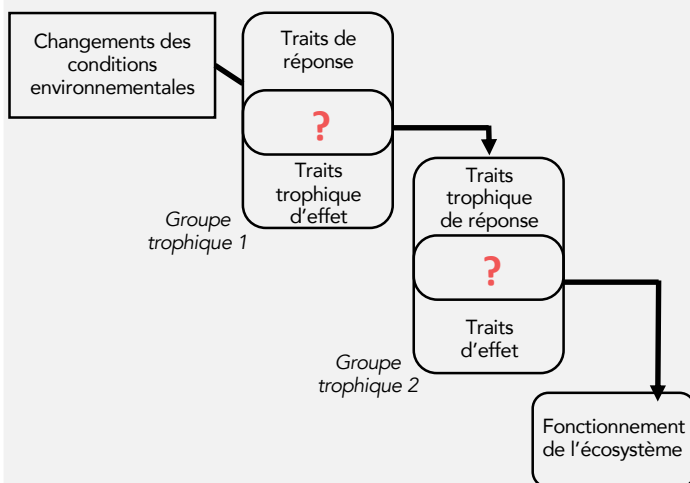
4. Vers une théorie généralisée de l'économie des systèmes plantes-sol ?

Dans les sols, la **stœchiométrie des nutriments** est déterminée par la qualité de la litière issue des plantes, et détermine l'investissement enzymatique des microbes (Li et al, 2019, Sinsabaugh 2009). Le compromis entre économie lente et rapide pourrait donc s'étendre à tout le système plantes-sol et son fonctionnement.



3. Des traits pour décrire les interactions entre niveaux trophiques (d'après Lavorel, 2013)

Certaines fonctions écosystémiques (ex. décomposition) dépendent des interactions entre plusieurs niveaux trophiques, que l'on peut décrire via les **traits d'interaction**



Troisièmement, il est nécessaire de passer de la mesure des mécanismes individuels par lesquels les espèces participent aux cycles biogéochimiques à des mesures de fonctionnement qui peuvent être réalisées à l'échelle des écosystèmes et de façon spatialement explicite. En effet, le focus de la modélisation du fonctionnement des écosystèmes se situe au niveau des écosystèmes dans leur ensemble, plutôt qu'au niveau des parties qui les constituent (ex. les organismes et leurs activités individuelles, Jax, 2005). On veut pouvoir décrire un 'état' de l'écosystème et de ses multiples composantes par la somme des processus qui le régissent (ESA, Naeem *et al.*, 1999; Reiss, Bridle, Montoya, & Woodward, 2009). Cependant, le fonctionnement des écosystèmes n'est pas restreint aux cycles biogéochimiques (Jax, 2005). Par exemple, en plus de leur rôle sur les cycles biogéochimiques, les plantes constituent un refuge pour de nombreuses espèces, ce qui participe au fonctionnement de l'écosystème. L'enjeu est donc d'identifier et mesurer tous les processus essentiels au fonctionnement des écosystèmes, indépendamment des organismes qui les réalisent (Manning *et al.*, 2018). On appelle donc fonction écosystémique toute variable mesurable à l'échelle de l'écosystème qui permet d'en caractériser son état (par exemple, des variables liées à la qualité de l'habitat, au lessivage des nutriments, à la productivité). Enfin, ce changement de perspective est nécessaire pour pouvoir quantifier l'importance relative de l'environnement et des communautés de plantes et du sol pour le fonctionnement des écosystèmes dans son ensemble.

II. Vers une prise en compte de l'environnement : utilisation de gradients d'altitude pour comprendre la réponse des plantes et de la biodiversité du sol aux changements environnementaux.

A. Les gradients d'altitude peuvent servir d'expérience naturelle pour comprendre la réponse des écosystèmes aux changements environnementaux.

Les variations spatiales des conditions environnementales (ex. climat, propriétés physico-chimiques du sol) le long de gradients naturels, et en particulier d'altitude, peuvent être utilisées pour mieux comprendre comment les assemblages et les activités biologiques des plantes et de la biodiversité du sol dépendent de l'environnement (Sundqvist, Sanders, & Wardle, 2013).

Tout d'abord, la comparaison de sites naturels caractérisés par différentes conditions environnementales, qu'on utilise comme différents traitements, permet de donner une idée de l'effet à long terme de l'environnement sur les assemblages et les activités biologiques des plantes et de la biodiversité sol.

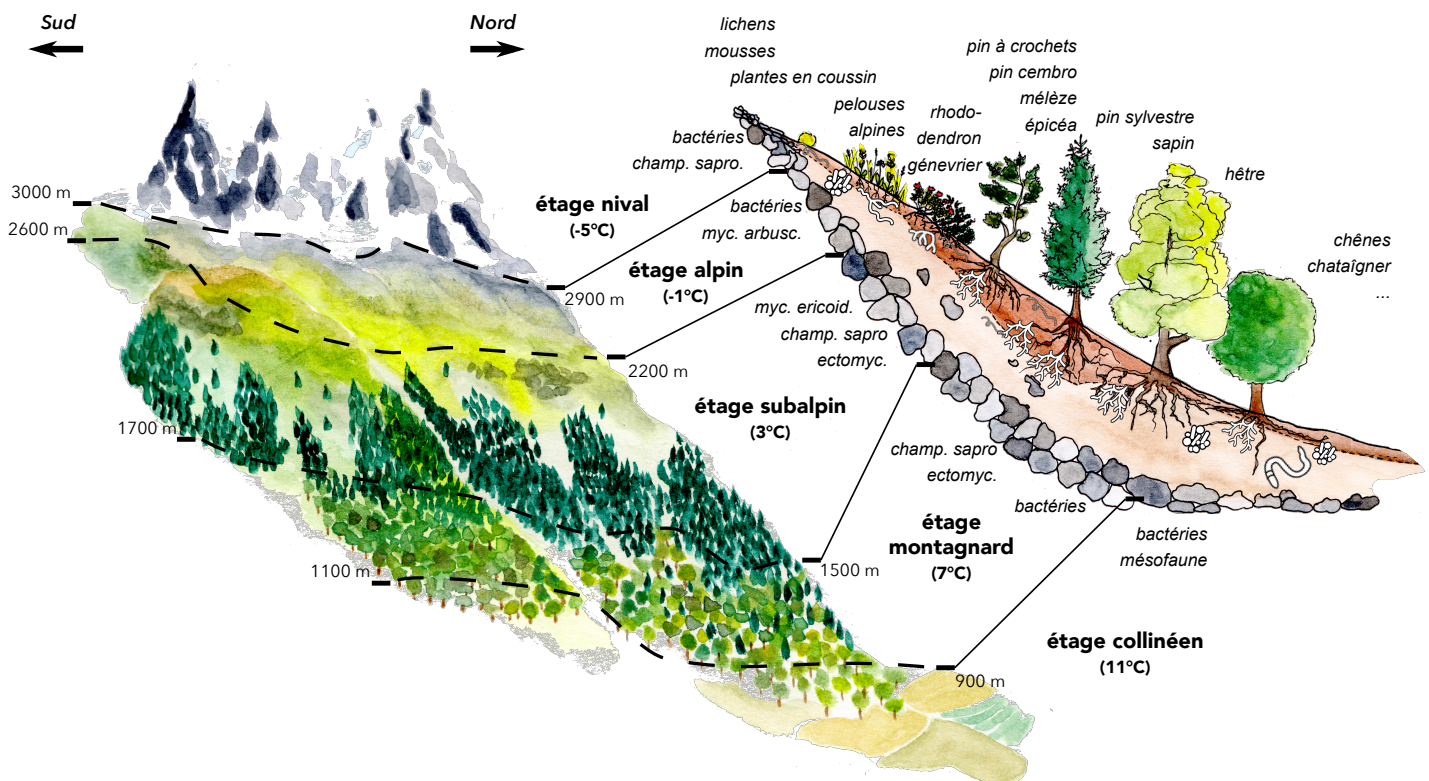


Figure 4| Étagement climatique dans les Alpes, et changements de composition (turnover) de la communauté de plantes et du sol le long d'un gradient d'altitude. Les gradients d'altitudes combinent une diminution constante de température avec l'altitude à des variations d'orientation, de pente et de topographie : ils offrent donc un large éventail de microclimats. Des crêtes ventées, vite déneigées et exposées à des variations extrêmes de températures jusqu'aux combes enneigées très tard dans l'été, chacun de ces microclimats héberge un système plantes-sol différent, avec des changements importants à la fois de la végétation, des organismes et de la physico-chimie du sol dans des espaces relativement réduits. Partie à droite d'après Hagedorn (2019).

En effet, la plupart des dynamiques écologiques qui conduisent un assemblage de plantes et d'organismes du sol dans un environnement donné s'étalent sur des décennies, voire des siècles ou millénaires, en tout cas sur des durées difficiles à étudier dans le cadre d'expériences contrôlées (Fukami & Wardle, 2005).

De plus, selon le principe de la substitution indirecte du temps par l'espace (indirect space-for-time substitution), on peut utiliser des sites naturels alignés le long d'un gradient d'altitude pour étudier les effets du réchauffement climatique sur les plantes et la biodiversité du sol (Fukami & Wardle, 2005). En effet, la température décroît linéairement avec l'altitude (Körner, 2003; Sundqvist *et al.*, 2013). Le long d'un gradient d'altitude, on peut donc mettre en place une expérience de façon à ce que les différences de température entre les sites soient comparables à l'ampleur du réchauffement climatique causé par les activités humaines. Comme les espèces présentes sur chaque site au sein d'un même gradient sont issues d'un même groupe d'espèces caractéristiques de la région, on peut considérer que les différences entre les assemblages de plantes et du sol de ces sites sont majoritairement dues aux différences de température entre les sites (Fukami & Wardle, 2005).

Cependant, si on s'intéresse à un seul gradient d'altitude, il est souvent difficile de différencier les effets de la température de ceux d'autres variables environnementales (ex. physico-chimie du sol), et de l'impact de l'histoire biogéographique des espèces, qui peuvent aussi plus ou moins co-varier avec l'altitude (Körner, 2007). Cette difficulté peut être partiellement surmontée grâce à l'utilisation de plusieurs gradients d'altitude au sein de la même région, puisque que la température et les autres facteurs abiotiques ne varient pas forcément avec l'altitude de la même manière au travers différents gradients d'altitude (bien que certaines variables, comme la longueur de la saison de végétation, restent très corrélées à la température, Fukami & Wardle, 2005; Körner, 2007). L'étude des assemblages de plantes et d'organismes du sol le long de plusieurs gradients d'altitude permet donc de dé-corréler les différents facteurs abiotiques et d'identifier des tendances de leurs effets à large échelle.

B. L'étude des liens entre environnement et plantes et biodiversité du sol présente un intérêt particulier dans les écosystèmes alpins.

Dans cette thèse, on a choisi d'échantillonner plusieurs gradients d'altitude dans les Alpes. Les écosystèmes de montagne sont particulièrement pertinents pour étudier les effets de l'environnement sur les plantes et la biodiversité du sol :

Premièrement, les écosystèmes alpins permettent d'étudier une grande variété de systèmes plantes-sol, qui vont d'écosystèmes de forêts mixtes à une quasi-absence d'espèces de plantes et de sol, en passant par des prairies et landes alpines (Figure 4). Cette diversité de systèmes plantes-sols est due à la longueur des gradients d'altitude dans les Alpes (300 à 4000m), qui, parce qu'ils sont corrélés à une diminution de la température, entraînent un étagement de la végétation (Figure 4).

Parallèlement, les Alpes sont caractérisées à chaque étage de végétation par une multitude de micro-écosystèmes avec des propriétés physico-chimiques du sol très variées, ce qui nous permettra de bien différencier les effets du climat et du sol sur les plantes et les organismes du

sol. En effet, au gradient de température, s'ajoutent une très forte hétérogénéité des sous-couches géologiques, des différences d'exposition, de pente, et de durée d'enneigement entre les surfaces et les combes, qui contraignent les propriétés physico-chimiques du sol (Figure 4, Choler, 2005; Körner, 2003; Schöb, Kammer, Choler, & Veit, 2009).

Enfin, les écosystèmes alpins sont à la fois particulièrement sensibles aux changements globaux et particulièrement importants pour les cycles biogéochimiques à large échelle. Ils sont ainsi plutôt froids en moyenne (on perd 0.6°C par rapport à la plaine tous les 100 mètres d'altitude), ce qui ralentit tous les processus biologiques. En particulier, la décomposition de la matière organique y est peu rapide. Pour l'instant, les écosystèmes alpins sont plutôt considérés comme des puits de carbone (jusqu'à 90 % de carbone stocké dans la zone alpine, Hagedorn, Gavazov, & Alexander, 2019). Cependant, de plus en plus d'études montrent que le réchauffement climatique est amplifié en altitude, ce qui pourrait porter les prédictions d'augmentation de 2 à 4 degrés au cours de siècle à 4 ou 8 degrés (Pepin *et al.*, 2015, www.creamontblanc.org). Une telle augmentation des températures pourrait faire remonter les différents assemblages de plantes et d'organismes du sol qui caractérisent les étages de végétation plus haut en altitude, avec des conséquences encore mal comprises sur les cycles biogéochimiques et le climat à large échelle (Carlson *et al.*, 2017). En haute altitude notamment, les sols (ex. le permafrost) ont souvent des proportions importantes (jusqu'à 60 %) de matière organique facile à décomposer, mais qui restent protégées grâce au froid (Hagedorn *et al.*, 2019). Une levée des contraintes de température pourrait favoriser l'installation d'espèces de plantes et du sol en altitude, et surtout, favoriser leur activité biologique (Bardgett, Freeman, & Ostle, 2008; Looby & Martin, 2020; Winkler *et al.*, 2018). Cela transformerait probablement les sols d'altitude en sources nettes de carbone atmosphérique (Bardgett *et al.*, 2008; Hagedorn *et al.*, 2019). La possibilité qu'une boucle de rétroaction positive entre les plantes, l'activité microbienne et le climat puisse se mettre en place avec le réchauffement climatique dans les écosystèmes alpins rend l'étude des liens entre environnement, plantes et sols particulièrement urgente dans ces écosystèmes (Bardgett *et al.*, 2008; Hagedorn *et al.*, 2019).

C. ORCHAMP – un observatoire spatio-temporel de la biodiversité et du fonctionnement des écosystèmes de montagne

Cette thèse s'appuie sur un observatoire appelé ORCHAMP, qui a été créé pour pouvoir observer, comprendre et modéliser les écosystèmes de montagne dans l'espace et le temps (orchamp.osug.fr). Coordonné par le LECA, il est géré de manière collective grâce à la participation active des acteurs locaux, des gestionnaires et des chercheurs dans le but de mieux préserver les écosystèmes de montagne. Cet observatoire est construit autour de multiples gradients d'altitude (de 800 à 2000 m de variation d'altitude) représentatifs des conditions climatiques et des propriétés du sol des Alpes françaises. Chaque gradient est constitué de parcelles permanentes qui se répartissent de la vallée au sommet, tous les 200 mètres d'altitude (Figure 5). Cet observatoire nous permettra de démêler les effets du climat et du sol sur les plantes et la biodiversité du sol et leur contribution aux cycles biogéochimiques à large échelle.

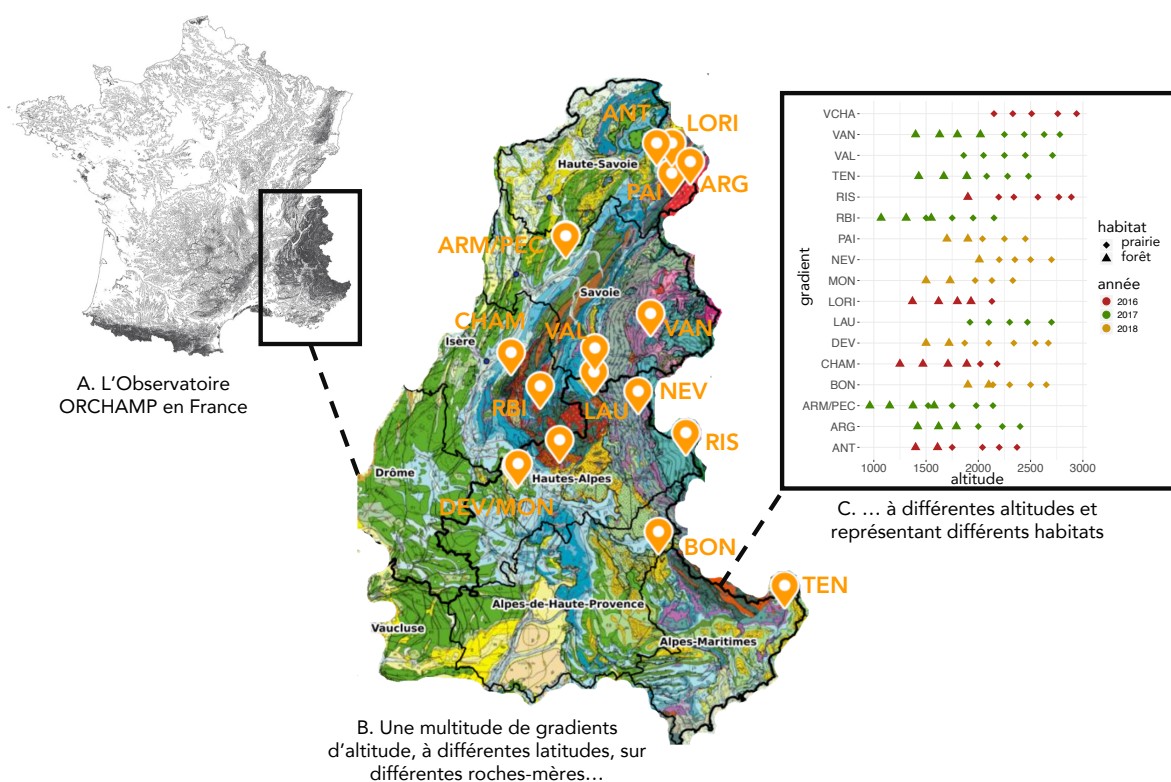


Figure 5 | ORCHAMP, un observatoire spatio-temporel de la biodiversité multi-échelles. Sur les 27 gradients actuellement suivis, seuls sont représentés les gradients utilisés au cours de ma thèse.

III. Adopter une approche multi-trophique pour passer des activités biologiques des organismes à la quantification de la contribution des communautés de plantes et du sol aux processus biogéochimiques.

A. Les plantes comme modèle d'étude historique des liens entre communautés et processus biogéochimiques.

En écologie, une communauté est un assemblage d'espèces différentes qui partagent une aire géographique, un environnement commun. Le concept est issu de l'idée qu'un ensemble de filtres opérant à différentes échelles sélectionnent les espèces d'une communauté locale, à partir d'un certain nombre d'espèce présentes dans la région de par leur histoire biogéographique (Figure 6, Keddy, 1992; Thuiller *et al.*, 2013). En particulier, ce cadre conceptuel fait l'hypothèse qu'à la fois des facteurs abiotiques (ex. climat, propriétés physico-chimiques du sol, Figure 6, E.) et biotiques (par ex : compétition, interactions trophiques, Figure 6, D.) peuvent influencer la composition de la communauté locale réalisée, via la niche des espèces. L'environnement abiotique sélectionne les espèces adaptées aux conditions locales. Les interactions biotiques déterminent également quelles espèces de cette sélection locale peuvent coexister au sein de la communauté locale (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012).

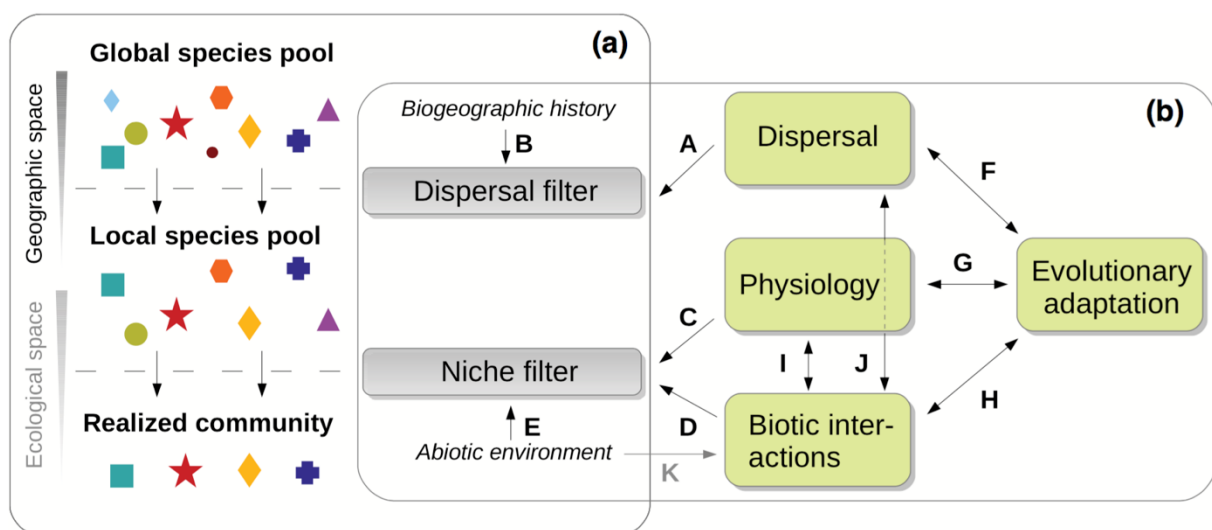


Figure 6, issue de Thuiller *et al.*, 2013 | (a) Représentation des filtres écologiques qui structurent les communautés locales réalisées. (b) Processus principaux qui influencent la structure des communautés et leurs effets directs (A-E) et indirects sur les filtres écologiques.

Dans la pratique on s'intéresse souvent à des communautés restreintes à un certain sous-ensemble de taxa, qui sont liés par des interactions de compétition ou de facilitation. Historiquement, par exemple, les écologues se sont beaucoup intéressés aux communautés de plantes. Notamment, le champ de recherche Biodiversité - Fonctionnement des Ecosystèmes (Biodiversité Ecosystem Functioning) a extensivement exploré la relation entre la diversité des communautés plantes et la productivité primaire nette, entre autres par le biais d'expériences manipulant la richesse des communautés de plantes (Axmanová *et al.*, 2013; Grace *et al.*, 2016;

Mueller, Tilman, Fornara, & Hobbie, 2013; van Ruijven & Berendse, 2009; Waide *et al.*, 1999). Ces expériences ont permis d'atteindre un consensus en écologie (Hooper *et al.*, 2005), qui indique que les communautés avec un plus grand nombre d'espèces utilisent et transforment les ressources abiotiques plus efficacement, et accumulent plus de biomasse que les écosystèmes appauvris par les extinctions d'espèces (Schleuning *et al.*, 2015). Ces expériences ont également permis de proposer des mécanismes qui pourraient expliquer la plus grande efficacité des communautés les plus riches. Ainsi, la plus grande efficacité des communautés les plus riches pourrait être due à : i/ des effets d'échantillonnage (c'est-à-dire une augmentation de la probabilité d'avoir une espèce très efficace dans une communauté plus riche), ii/ des effets de complémentarité (c'est-à-dire une utilisation plus complète des ressources dans les communautés plus riches, parce que chaque espèce utilise une partie différente des ressources) et iii/ des interactions interspécifiques (facilitation, Hines *et al.*, 2015; Hooper *et al.*, 2005; Loreau *et al.*, 2001; Schleuning *et al.*, 2015).

Cependant, à richesses taxonomiques égales, deux communautés de plantes ne produisent pas forcément la même quantité de biomasse. La richesse taxonomique n'est donc pas un très bon descripteur des communautés, et ni un très bon prédicteur de leur contribution aux processus biogéochimiques. Cela est dû au fait que cette mesure ne prend ni en compte les caractéristiques spécifiques des espèces, ni comment elles sont assemblées dans la communauté (leur composition). Dans les années 2000, Lavorel & Garnier ont proposé un cadre conceptuel qui s'appuie sur la notion de traits fonctionnels, en définissant deux types de traits : la présence d'une espèce dans une communauté dépend de ses traits de réponse, tandis que sa contribution à un processus biogéochimique dépend de ses traits d'effet (Box 2, Lavorel & Garnier, 2002; Violle *et al.*, 2007). Par exemple, à l'échelle d'une communauté de plantes, la productivité primaire nette est le résultat d'une succession de plusieurs filtres environnementaux et biotiques, qui en sélectionnant des individus avec des réponses appropriées, déterminent une composition de traits fonctionnels. Dans cet exemple, on peut utiliser la taille, qui est corrélée à la biomasse (standing biomass) de la plante, et la quantité de matière sèche des feuilles (Leaf Dry Matter Content), qui est liée au taux de croissance, deux termes importants dans l'équation de la productivité primaire nette (Box 2, Lavorel & Garnier, 2002). À l'échelle de la communauté, prendre en compte la composition concernant ces deux traits permet de grandement améliorer les prédictions de la productivité primaire nette. Ainsi, les mesures de diversité fonctionnelles (ex. les volumes fonctionnels, les moyennes de traits pondérées à l'échelle de la communauté), qui prennent en compte la composition en traits d'effet de la communauté de plantes, permettent de mieux comprendre la contribution des communautés de plantes aux processus biogéochimiques, et d'en améliorer les prédictions (Garnier *et al.*, 2004; Lavorel & Garnier, 2002).

B. Limites et lacunes des approches appliquées aux communautés de plantes

Tout d'abord, l'utilisation de la richesse taxonomique ou des mesures de diversité fonctionnelle comme descripteurs des communautés n'est pas toujours facile à généraliser à d'autres groupes d'organismes. Notamment, ces mesures sont peu adaptées à l'étude des organismes du sol (Kardol, Throop, Adkins, & Graaff, 2016; Thakur & Geisen, 2019; Thakur *et al.*, 2020; Van Der Heijden, Bardgett, & Van Straalen, 2008; Wall *et al.*, 2010). En effet, la diversité des organismes du sol et de leurs traits fonctionnels est immense, et la richesse estimée des grands groupes d'organismes du sol diffère de plusieurs ordres de grandeur (Box 1, Adl *et al.*, 2007; Hawksworth & Lücking, 2017; Louca *et al.*, 2019; Poinar Jr., 2012; Thibaud & D'Haese, 2010; Walter & Proctor, 2013). La profondeur des connaissances taxonomiques de la biodiversité du sol varie beaucoup selon les grands groupes taxonomiques étudiés ou leur classe de taille (Box 1), et les connaissances sur leurs traits fonctionnels sont souvent quasiment inexistantes (T. W. Crowther *et al.*, 2019; Green, Bohannan, & Whitaker, 2008; Wall *et al.*, 2010). De plus, le sol est un habitat extrêmement hétérogène, et la majorité des organismes du sol se concentrent dans des pores de tailles variables, mais généralement très petits (ex. de l'ordre du millimètre à la dizaine de centimètres, Box 1, Lavelle, 2004). Il en résulte que les organismes du sol sont difficiles à observer et à échantillonner (Fierer, 2017). Par conséquent, il est difficile de les étudier ensemble dans les cadres conceptuels existants.

Cependant, les relations – trophiques ou non – qui lient les différents groupes d'organismes au sein des communautés naturelles de plantes et du sol peuvent influencer directement et indirectement les processus biogéochimiques, et ont souvent été ignorées par les premières études expérimentales et théoriques restreintes à un sous-ensemble de taxa (Hines *et al.*, 2015). En milieu naturel, les herbivores influencent directement et indirectement la productivité primaire des communautés de plantes, par exemple (Moretti *et al.*, 2013). Directement, en se nourrissant de la biomasse des plantes. Indirectement, en agissant comme un filtre biotique de la communauté végétale : les herbivores peuvent avoir des préférences alimentaires marquées pour certaines plantes caractérisées par des traits qu'ils apprécient. Ils favorisent ainsi des plantes avec des traits de résistance aux herbivores, modifient la composition de la communauté végétale et par là, la composition en traits d'effet liés à la productivité primaire (Box 1, Ibanez, Lavorel, Puijalon, & Moretti, 2013). De plus, pour continuer avec l'exemple de la productivité primaire, les liens indirects entre plantes et organismes du sol mentionnés en première partie peuvent également avoir une influence directe et indirecte : les décomposeurs influencent la disponibilité en nutriments dans le sol, ce qui peut directement favoriser ou défavoriser la production de biomasse végétale, et indirectement modifier la composition des communautés végétales en sélectionnant des plantes avec des traits plus exploitatifs (disponibilité en nutriments élevée), ou plus conservatifs (disponibilité en nutriments faibles, Box 2). Il est donc nécessaire de prendre en compte les réseaux d'interactions qui lient les plantes et organismes du sol pour prédire correctement la réponse aux changements environnementaux des communautés de plantes et du sol, ainsi que leur contribution aux processus biogéochimiques.

C. Combiner échantillonnage des organismes du sol par métabarcoding, approche multi-trophique, et mesures de composition pour prendre en compte les communautés du sol.

1. Le métabarcoding de l'ADN environnemental pour améliorer les connaissances taxonomiques dans le sol.

Les techniques d'identification des espèces par l'ADN constituent une avancée majeure pour l'étude des communautés du sol dans leur globalité, car elles apportent une solution (partielle) aux problèmes que posent l'échantillonnage et l'identification des organismes du sol. Le métabarcoding, notamment, désigne l'identification de multiples taxons (au niveau de l'espèce ou à d'autres niveaux dans la taxonomie) via l'utilisation d'ADN total et généralement dégradé extrait d'un échantillon environnemental (ex. de sol, Taberlet & Coissac, 2012; Taberlet, Coissac, Hajibabaei, & Rieseberg, 2012). On peut également considérer les identifications faites à partir d'organismes entiers ou d'organes isolés comme métabarcoding. Dans son état actuel, la technique s'appuie sur une étape d'amplification par PCR (Polymerase Chain Reaction), qui crée de multiples copies des fragments d'ADN et permet ainsi de détecter un signal à partir des très petites quantités d'ADN présentes dans les échantillons environnementaux. Ces copies doivent ensuite être séquencées, ce qui explique pourquoi l'émergence du métabarcoding de l'ADN a été grandement facilitée par le développement des plateformes de séquençage à haut-débit (NGS, Next Generation Sequencing). Cependant, la PCR génère beaucoup d'erreurs et les données doivent ensuite être nettoyées (Taberlet & Coissac, 2012; Zinger *et al.*, 2019). Cela est fait via des traitements bio-informatiques, au cours desquels on rassemble les séquences similaires en Unités Moléculaires Taxonomiques Opérationnelles (Molecular Operational Taxonomy Units, MOTUs), que l'on espère représentatifs des espèces de l'échantillon. Le métabarcoding est principalement limité par sa dépendance à la PCR et par le travail considérable qui est nécessaire pour constituer des bases de références taxonomiques. Mais malgré ses limites, la technique a nettement amélioré la connaissance des communautés du sol (T. W. Crowther *et al.*, 2019). Elle a notamment permis de remettre en cause l'absence de biogéographie chez les micro-organismes (Chu, Gui-Feng, Ma, Fan, & Delgado-Baquerizo, 2020), et a grandement contribué à l'identification de patrons de diversité à l'échelle globale pour les bactéries (Fierer & Jackson, 2006), les champignons (Tedersoo *et al.*, 2014), et les protistes (Bates *et al.*, 2013). Enfin, en facilitant l'échantillonnage et l'identification des espèces des micro-organismes à la faune du sol, elle ouvre la voie à des études qui, comme cette thèse, prennent en compte la communauté du sol dans son ensemble, à de larges échelles spatiales.

2. L'approche multi-trophique des communautés : regrouper les espèces qui ont des rôles similaires dans la communauté pour pouvoir prendre en compte leurs interactions trophiques

Bien que le développement des méthodes de séquençage haut-débit et du métabarcoding permettent de mieux appréhender la diversité taxonomique et de mieux caractériser la composition de la communauté du sol, il reste difficile de quantifier sa contribution aux cycles biogéochimiques, notamment à cause de l'immense diversité des interactions biotiques qui relient les organismes du sol. Pour réduire la complexité de la communauté du sol, les écologues ont historiquement groupé les espèces du sol en fonction de caractéristiques communes, notamment : i/ de manière taxonomique (par exemple, au sein des vers de terre, des collemboles ou des nématodes) ; ii/ en fonction de leur taille (c'est-à-dire la macro-, la méso- et la microfaune comme présentés dans la première partie, Gobat, Aragno, & Matthey, 1998) ; iii/ en fonction des similitudes de leurs traits de réponse et/ou d'effet (Bouché, 1977) ; iv/ en groupes trophiques (De Ruiter, Neutel, & Moore, 1996). Si l'agrégation des espèces du sol selon leur taxonomie, leur taille ou leurs traits de réponse et d'effet ne permet qu'une approximation indirecte de la place des espèces du sol dans la communauté, l'agrégation en groupes trophiques, en revanche, permet de mieux prendre en compte les interactions trophiques entre les espèces du sol (Gauzens, Thébault, Lacroix, & Legendre, 2015; O'Connor *et al.*, 2020).⁴

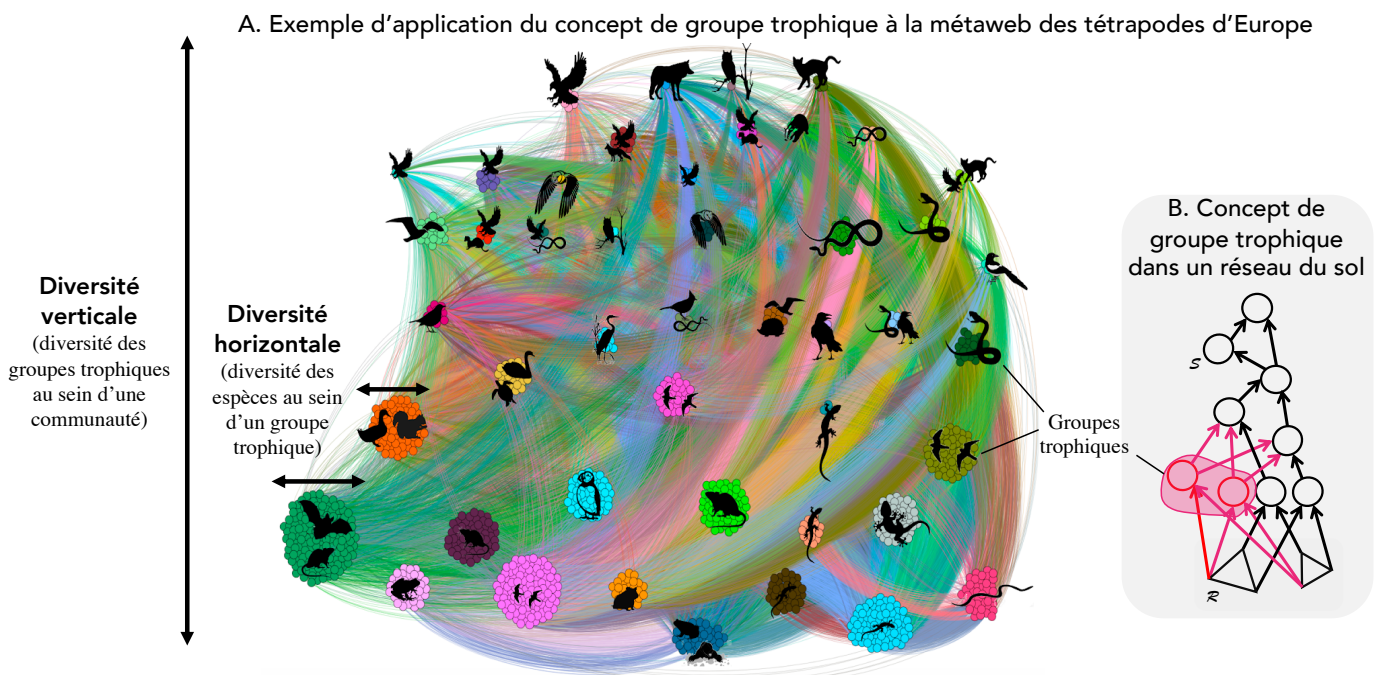


Figure 7 | Le concept de groupe trophique (niche eltonienne) appliqué à différents types de réseaux trophiques. (A.) Application à la métaweb⁴ des tétrapodes d'Europe (d'après O'Connor *et al.*, 2020, article dont je suis co-auteur). Chaque cercle de couleur représente une espèce. Les espèces sont rassemblées en groupes trophiques, selon leur niche eltonienne, ce qui permet de grandement simplifier la métaweb. Appliqué au réseau du sol (B.), ce concept doit s'élargir pour inclure des ressources (triangles, **R**) qui ne sont pas des espèces (cercles, **S**). Les espèces d'un même groupe trophique partagent ressources et consommateurs (flèches et zone en rose).

⁴ Métaweb : réseau trophique représentant les interactions trophiques potentielles entre les espèces (ici les tétrapodes d'Europe), construit à partir de connaissances d'experts et de la littérature.

Au sein des groupes trophiques en effet, les espèces sont regroupées selon leur statut dans la communauté, leur niche eltonienne, définie de la façon suivante :

“It is therefore convenient to have some term to describe the status of an animal in its community, to indicate what it is doing and not merely what it looks like, and the term used is niche. Animal have all manner of external factors acting upon them (...) and the niche of an animal means its place in the environment, its relation to food and enemies.” Elton (1927)

En considérant comme équivalentes les espèces qui ont la même place dans l’environnement, ainsi que des proies (ou si on l’applique aux organismes du sol, des ressources) et des consommateurs similaires, les groupes trophiques permettent de simplifier la représentation des réseaux trophiques et de s’affranchir de leur complexité dans les données empiriques, tout en prenant en compte à la fois la composition en espèces de la communauté et les interactions trophiques qui lient ces espèces (Figure 7, O’Connor *et al.*, 2020; Thompson *et al.*, 2012). De plus, ils regroupent en général des espèces qui ont des traits fonctionnels assez proches (O’Connor *et al.*, 2020).

Adopter une approche multi-trophique - c’est-à-dire considérer plusieurs groupes trophiques de la communauté du sol en même temps - présente donc un intérêt particulier pour quantifier la contribution de la communauté de plantes et du sol aux cycles biogéochimiques. On peut notamment décrire la diversité multi-trophique de la communauté de plantes et du sol, à travers trois concepts. Premièrement, la diversité totale correspond à la diversité de la communauté indépendamment des groupes trophiques qu’elle contient (e.g richesse spécifique de la communauté). Deuxièmement, la diversité verticale, parfois appelée diversité trophique, correspond à la diversité des rôles trophiques de la communauté (ex. le nombre de groupes trophiques, Figure 7, Bascompte, García, Ortega, Rezende, & Pironon, 2019; Hines *et al.*, 2015). Enfin, la diversité horizontale correspond à la diversité au sein des groupes trophiques (ex. richesse spécifique des plantes, Figure 7). Dans cette thèse, on appliquera ces trois concepts aux communautés de plantes et du sol au sein de modèles graphiques (ex. modèles d’équation structurelles, Box 3), afin d’identifier les mécanismes qui lient la communauté de plantes et du sol aux cycles biogéochimiques, le long de gradients environnementaux.

3. Approcher la composition des groupes trophiques

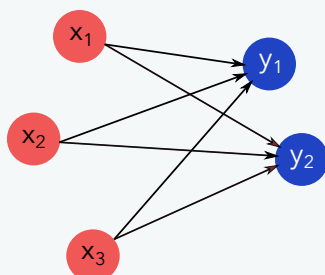
Enfin, l'utilisation des indices de diversité et des méthodes statistiques qui prennent en compte la composition en espèces des différents groupes trophiques au sein de la communauté de plantes et du sol, peut permettre de s’affranchir des limites de la richesse taxonomique, de contourner les difficultés liées à la méconnaissance des traits de réponse et d’effet des organismes du sol, et d’approximer la composition en traits d’effet au sein de ces groupes. Premièrement, les indices de β -diversité permettent de caractériser des changements de composition entre différents sites, notamment par paires de sites, via l’utilisation d’indices de dissimilarité (Baselga, 2010; Ohlmann *et al.*, 2018, 2019). L’utilisation de méthodes statistiques multivariées (ex. Analyse Factorielle des Correspondances) permet également de résumer les principaux axes de variation des compositions des communautés entre plusieurs sites (Piton *et al.*, 2020). Enfin, les modèles de distribution multi-espèces permettent de modéliser les

distributions de plusieurs espèces en même temps, et donc de prédire la composition des communautés dans des conditions environnementales données (Pollock, Morris, & Vesk, 2012).⁵

Les modèles utilisés dans ma thèse ont en commun de chercher à **inférer des relations entre variables** en mesurant leurs corrélations partielles. Une corrélation partielle correspond à la corrélation entre deux variables a et b lorsqu'on contrôle l'effet d'une troisième variable c (ou plus).

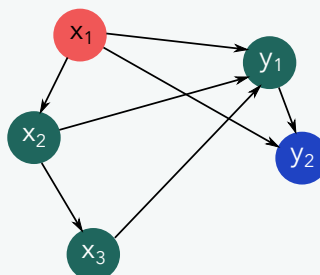
Cependant, ils sont assez différents, notamment en ce qui concerne les éléments suivants :

Modèle linéaire mixte



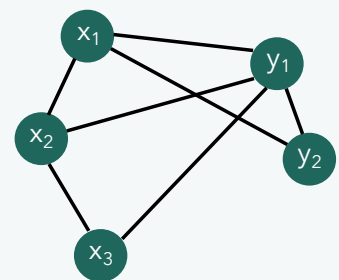
- Modèle **dirigé**.
- Plusieurs **prédicteurs** (oranges) expliquent une ou plusieurs **variables réponse** (bleues). Si il y a plusieurs **variables réponse**, elles sont **indépendantes**.
- On a de forts *a priori* sur les prédicteurs. On cherche à **quantifier les effets** de ces prédicteurs (test d'hypothèse).
- Modèle avec un **seul** « niveau » (i.e. uniquement des liens directs).

Modèle d'équations structurelles



- Modèle **dirigé**.
- Certaines variables peuvent être à la fois des prédicteurs et des variables réponse. On parle donc de **variables exogènes** (oranges, qui correspondent aux variables uniquement prédicteurs), et de **variables endogènes** (vertes et bleues, qui correspondent aux variables uniquement de réponse et à la fois prédicteurs et de réponse).
- On a de forts *a priori* sur les effets des variables les unes sur les autres, i.e. sur **la structure causale** des liens entre les variables. On cherche à la fois à **tester** si ces *a priori* sur **la structure** du graphe⁵ sont vrais (test d'hypothèse) et à **quantifier les liens directs et indirects** entre les variables.
- Modèle avec **plusieurs** « niveaux » (i.e. on peut avoir des liens indirects).

Graphical Lasso



- Modèle **non-dirigé**.
- Parce que le modèle est non-dirigé, il n'y a plus de variables exogènes et/ou endogènes : on ne parle plus que des **nœuds** (verts) du graphe.
- **On n'a pas d'a priori** sur les liens entre les variables. On cherche à inférer la structure d'un graphe où certains liens sont absents (i.e. clairsemé, *sparse*). En d'autres termes, on cherche à faire une carte des liens entre variables.
- Modèle avec **plusieurs** « niveaux »

Box 3 | Comparaison des modèles linéaires mixtes avec deux types de modèles graphiques, les modèles d'équations structurelles et le Graphical Lasso

⁵ Graphe : objet formé par un ensemble de nœuds (variables) et d'arêtes (liens).

IV. Vers une approche spatiale du fonctionnement des écosystèmes

A. *Le concept de fonctionnement de l'écosystème, intrinsèquement lié à l'Homme ...*

L'origine du concept de fonctionnement des écosystèmes se trouve dans le constat de l'accélération de la disparition des espèces vivantes, et dans la volonté de prédire les conséquences de l'érosion de la biodiversité pour l'Homme.

Ainsi, dans la préface de leur livre *Extinction* publié en 1981, Paul et Anne Ehrlich comparent les différentes espèces biologiques à des rivets qui maintiennent ensemble les ailes d'un avion (symbolisant les écosystèmes de la terre), dans lequel l'Homme est embarqué. Mais en même temps, la compagnie aérienne paie une personne pour qu'elle enlève les rivets des ailes un par un, afin de les vendre pour faire du profit. Cette personne ne semble pas être très inquiète :

"Don't worry', he assures you. 'I am certain the manufacturer made this plane much stronger than it needs to be, so no harm's done. Besides, I've taken lots of rivets from this wing and it hasn't fallen off yet. [. . .] As a matter of fact, I am going to fly on this flight also, so you can see there's absolutely nothing to be concerned about.'" Ehrlich & Ehrlich (1981)

Cette image, qui préfigure la création du champ de recherche Biodiversité-Ecosystem Functioning et du concept de fonctionnement de l'écosystème, met également le lien à l'Homme en évidence : puisque nous sommes embarqués dans l'avion, il est urgent d'évaluer l'état de l'avion, de quantifier le risque que l'on prend à laisser l'ouvrier enlever des rivets, et de prédire à quel moment l'avion va tomber.

B. *... constitue un changement de perspective par rapport aux cycles biogéochimiques ...*

Le concept de fonctionnement des écosystèmes constitue un changement de perspective par rapport à l'évaluation de la contribution des communautés de plantes et du sol aux processus biogéochimiques. En effet, au lieu de mettre l'accent sur un seul processus biogéochimique, on veut quantifier la contribution des différents groupes trophiques à plusieurs processus en même temps, pour pouvoir évaluer l'état global de l'écosystème. Les groupes trophiques apparaissent donc dans le contexte plus complexe de tout l'écosystème auquel ils appartiennent (Jax, 2010). En d'autres termes, on adopte une vision systémique, multidimensionnelle. Ce changement de perspective place la variable caractérisant le fonctionnement de l'écosystème (la fonction écosystémique) comme la variable réponse (y-axis), tandis que la biodiversité en devient un prédicteur (x-axis, Dooley *et al.*, 2015; Jax, 2010).

De plus, bien que certains auteurs restreignent le fonctionnement des écosystèmes aux processus biogéochimiques et aux flux de matière et d'énergie (Barnes *et al.*, 2014; Naeem & Wright, 2003), le concept présente l'avantage de pouvoir intégrer également d'autres fonctions mesurables à l'échelle de l'écosystème, et que l'on considère comme importantes pour caractériser son état. Par exemple, les processus strictement biologiques, liés aux interactions

ou aux cycles de vie (ex. pollinisation, bioturbation), ou certaines propriétés de l'écosystème lui-même sont souvent incluses dans les études qui s'intéressent au fonctionnement des écosystèmes (Boero & Bonsdorff, 2007; Maestre, Castillo-Monroy, Bowker, & Ochoa-Hueso, 2012; Schleuning *et al.*, 2015; Soliveres *et al.*, 2016; van der Plas *et al.*, 2016) .

Enfin, le besoin d'une mesure permettant d'avoir une compréhension globale du fonctionnement des écosystèmes émerge de cette vision holistique du fonctionnement des écosystèmes. En d'autres termes, on cherche une mesure intégrant les interrelations entre les différentes fonctions des écosystèmes et résumant la capacité de l'écosystème à remplir simultanément plusieurs fonctions écosystémiques. Le concept de multifonctionnalité, inventé pour remplir ce rôle, n'avait été défini jusqu'à récemment qu'au sens large, par 'la provision simultanée de multiples fonctions' (Byrnes *et al.*, 2014) ou 'le potentiel des paysages à fournir de multiples avantages à la société' (Mastrangelo *et al.*, 2014), ce qui mettait en évidence l'ambiguïté des objectifs de ce concept et de son lien à l'Homme. En 2018, Manning *et al.* proposent une redéfinition, pour tenter d'en séparer les deux aspects : d'une part, décrire objectivement le fonctionnement des écosystèmes 'sans jugement de valeur concernant le niveau ou les types de fonctions souhaités', et d'autre part, représenter les services rendus par les écosystèmes par rapport à la demande humaine. Ils définissent ainsi d'une part la multifonctionnalité des fonctions écosystémiques, qui intègre uniquement les fonctions écosystémiques et devrait constituer 'une mesure de la performance globale d'un écosystème', et d'autre part, la multifonctionnalité des services des écosystèmes, qui prend en compte uniquement les services des écosystèmes et où on assume le lien à l'homme en pondérant les services selon la demande humaine (Manning *et al.*, 2018). Dans cette thèse, je me suis concentrée sur la multifonctionnalité des fonctions écosystémiques, nommée par la suite multifonctionnalité pour rester simple. L'objectif ici, sans chercher à décrire une performance globale des écosystèmes, mais en ayant conscience de la subjectivité de certains choix dans les fonctions écosystémiques, était plutôt d'explorer les différentes pistes vers des cartographies et prédictions du fonctionnement des écosystèmes à large échelle.

C. ... qui permet de modéliser plus facilement le fonctionnement des écosystèmes de façon spatialement explicite et en fonction de l'environnement.

En effet, les fonctions écosystémiques, ainsi définies, permettent d'étudier facilement le fonctionnement des écosystèmes de façon spatialement explicite. De plus, elles peuvent être utilisées comme variables réponses au sein de modèles plus complexes, tels que les modèles d'équations structurelles. Ces modèles permettent d'évaluer l'effet des prédicteurs de façon hiérarchique et d'évaluer des liens directs et indirects (Figure 8, Box 3, Grace *et al.*, 2016; Shipley, 2016). Dans cette thèse, nous avons essayé de quantifier l'importance relative de l'environnement et de la communauté de plantes et du sol sur de multiples fonctions écosystémiques (ex. productivité, décomposition).

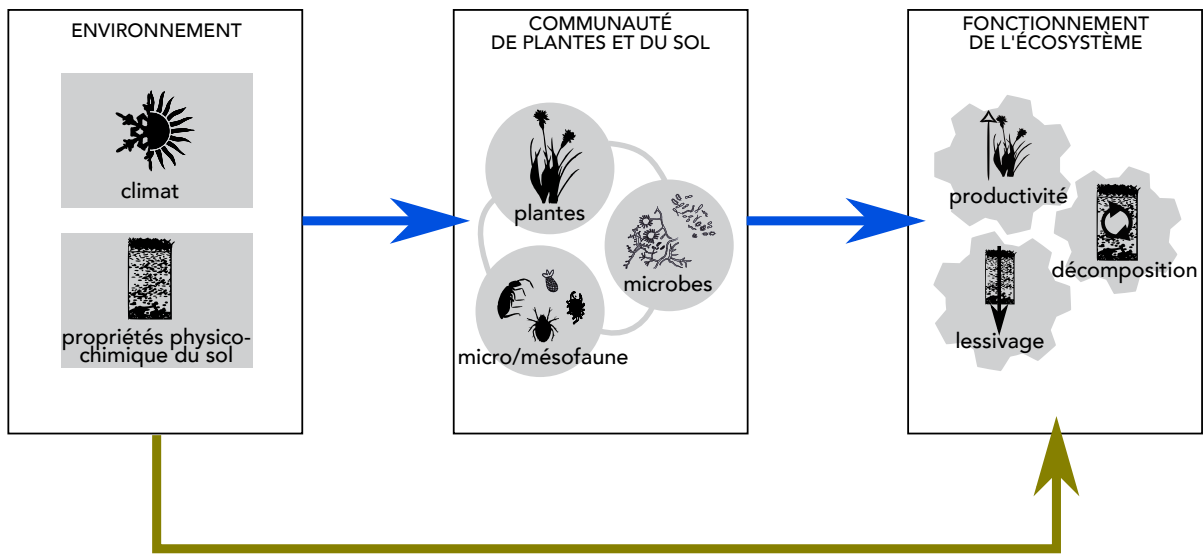


Figure 8 | Une vision hiérarchique des liens directs et indirects entre environnement, communauté de plantes et du sol et fonctionnement de l'écosystème. Dans cet exemple, la flèche verte représente le lien direct et les flèches bleues représentent le lien indirect, via la communauté de plantes et du sol, entre environnement et fonctionnement de l'écosystème.

V. Plan du manuscrit

Dans le cadre de cette thèse, qui se veut à la frontière entre biogéographie, écologie des communautés, écologie trophique et écologie fonctionnelle, je me suis intéressée à la modélisation dans l'espace géographique des liens entre environnement, diversité des communautés de plantes et du sol, et fonctionnement des écosystèmes.

Dans un premier temps (Chapitre 1), via l'utilisation d'une démarche systémique le long d'un gradient d'altitude dans les Alpes françaises, nous quantifions l'importance relative des changements environnementaux et de composition de la communauté de plantes et du sol pour le fonctionnement des écosystèmes. D'une part, ce chapitre révèle l'influence de certains groupes clés (ex. les champignons saprophytes) sur la productivité et la multifonctionnalité de l'écosystème. D'autre part, il souligne le rôle indirect joué par d'autres groupes trophiques qui interagissent avec les champignons saprophytes. Ainsi, ce premier chapitre soulève la question de l'existence d'une régulation de la diversité et de l'activité des groupes de décomposeurs (bactéries et champignons), via leur interaction avec les groupes trophiques qui les consomment.

Dans un second chapitre, nous répondons à cette question en modélisant hiérarchiquement le climat, le sol, les consommateurs de microbes, les bactéries, les champignons et leur activité de décomposition dans un modèle d'équation structurelles. En intégrant pour la première fois le réseau trophique du sol dans la modélisation d'une fonction écosystémique qui lui est associée, nous ouvrons la voie des prédictions spatiales du fonctionnement des écosystèmes. Cependant, la vision hiérarchique du lien entre environnement, diversité des plantes et du sol, et fonctionnement est difficile à appliquer dans les cas où il existe des rétroactions entre les fonctions écosystémiques et les groupes trophiques, ou entre les fonctions écosystémiques.

Dans une troisième partie (Chapitre 3), nous adoptons donc une démarche qui généralise le cadre conceptuel des traits fonctionnels de réponse et d'effet au contexte multi-trophique, et tentons d'identifier quels aspects de la communauté microbienne (ses traits ou sa fonction), permettent le mieux de prédire les distributions des communautés de plantes. Ce chapitre, qui révèle que l'effet de l'activité de décomposition microbienne est un bon prédicteur des distributions des plantes alors que les traits fonctionnels microbiens liés à l'acquisition des ressources n'ont pas d'effet significatifs, nous conduit dans une quatrième partie à remettre en question la vision hiérarchique du lien environnement-biodiversité-fonctionnement.

Dans ce dernier chapitre (Chapitre 4), à l'aide d'une approche non-dirigée, nous explorons les associations biogéographiques entre traits et fonction des organismes décomposeurs, et traits et fonction des plantes. Ce chapitre permet de confirmer l'importance de la qualité de la litière pour faire le lien entre les compartiments sous et sur le sol à large échelle.

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Productions académiques

Cette thèse s'appuie sur les articles suivants, publiés ou en préparation :

- **Martinez-Almoyna**, C., Thuiller, W., Chalmandrier, L., Ohlmann, M., Foulquier, A., Clément, J.C., *et al.* (2019). Multi-trophic β -diversity mediates the effect of environmental gradients on the turnover of multiple ecosystem functions. *Funct. Ecol.*, 33, 1365-2435.13393.
- **Martinez-Almoyna**, C., Saillard, A., Zinger, L., Lionnet, C., Foulquier, A., Gielly, L., *et al.* (2021). Differential effects of soil food webs on decomposition in mountain ecosystems. *to be submitted to Ecol. Lett.*
- **Martinez-Almoyna**, C., Piton, G., Abdulhak, S., Boulangeat, L., Choler, P., Delahaye, T., *et al.* (2020). Climate, soil resources and microbial activity shape the distributions of mountain plants based on their functional traits. *Ecography.*, 43, 1550–1559.
- Weil, S.-S., **Martinez-Almoyna**, C., Piton, G., Renaud, J., Boulangeat, L., Foulquier, A., *et al.* (2021). Strong links between plant traits and microbial activities but different abiotic drivers in mountain grasslands. *Revis. J. Biogeogr.*

Cet article est issu de la thèse de master de Sarah Weil, que j'ai co-encadrée avec l'aide de Tamara Münkemüller et Wilfried Thuiller. J'ai participé à la conceptualisation, à l'analyse et à la rédaction de cet article, dont elle est premier auteur. Cependant, cet article faisant partie intégrante de ma réflexion de thèse, j'ai considéré qu'il était intéressant de le discuter ici.

Par ailleurs, au cours de ma thèse, j'ai participé à l'élaboration des articles suivants (publiés ou en préparation), qui ne sont pas intégrés ici :

- O'Connor, L.M.J., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., **Martinez-Almoyna**, C., *et al.* (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *J. Biogeogr.*, 47, 181–192.

Cet article est issu du stage de césure de Louise O'Connor, j'ai participé à la conceptualisation de l'étude, et à sa rédaction. Cet article à un écho important dans ma thèse car il montre l'intérêt d'une méthode statistique (le *stochastic block model*) pour construire des groupes trophiques.

- Capowicz, Y., Jouquet, P., Blight, O.,..., **Martinez-Almoyna** C.,..., Hedde M. *et al.* (2021). Groups in soil ecology, could we do better than a Tower of Babel ? in prep.

Cet article est issu d'une réflexion sur les groupes trophiques du sol, engagée au début de ma thèse avec Sara Si-Moussi et Mickael Hedde, et reprise par des spécialistes du sol. Encore en préparation, il vise à proposer un cadre méthodologique pour standardiser les groupes trophiques du sol.

- Leitão, P.J., Andrew, C.J., Engelhardt, E.K., Graham, C.H., **Martinez-Almoyna**, C., Mimet, A., *et al.* (2020). Macroecology as a hub between research disciplines: Opportunities, challenges and possible ways forward. *J. Biogeogr.*, 47, 13–15.

Cet article est issu d'un workshop au cours de la conférence de macroécologie 'Macroecology in the era of Big Data' qui a eu lieu à Zürich en 2018.

Synopsis du premier chapitre

La recherche sur le lien entre environnement, biodiversité et fonctionnement des écosystèmes a déjà permis de nombreuses avancées. En 2006, la synthèse de plus de 100 études manipulant la diversité (généralement des plantes herbacées) a apporté la preuve expérimentale d'un effet positif de la diversité sur la productivité, alors que les développements théoriques et mathématiques ont par ailleurs permis de proposer des mécanismes explicatifs de ce lien. Plus récemment, plusieurs études ont montré que les changements indépendants de biodiversité au sein de plusieurs niveaux trophiques peuvent influencer le fonctionnement des écosystèmes. Cependant, de nombreuses questions subsistent : *Comment la variabilité spatiale des conditions environnementales en milieu naturel influence-t-elle les changements de biodiversité au sein de plusieurs groupes trophiques, et quelles sont les conséquences sur les fonctions écosystémiques ? Quelle est l'importance relative de l'environnement et de la biodiversité ? Quels sont les aspects les plus pertinents de la diversité multi-trophique ? Quelle est l'importance des interactions entre les groupes trophiques par rapport aux changements indépendants de diversité au sein des différents groupes trophiques ? Peut-on généraliser les mécanismes explicatifs des liens entre richesse des plantes et productivité primaire à d'autres fonctions écosystémiques, ou la multifonctionnalité des écosystèmes ?*

Ce premier chapitre aborde ces questions en adoptant une démarche systémique le long d'un gradient d'altitude dans les Alpes françaises. Nous quantifions comment les changements des conditions climatiques et édaphiques influencent les changements de diversité au sein de la communauté de plantes et du sol, et estimons les conséquences directes et indirectes sur de multiples fonctions écosystémiques ainsi que sur la multifonctionnalité. Nous caractérisons les changements de composition de la communauté de plantes et du sol le long du gradient d'altitude en combinant une approche multi-trophique et l'utilisation de la β -diversité. Nous comparons également la pertinence de trois mesures de diversité multi-trophique (totale, verticale et horizontale) dans l'étude du lien environnement-biodiversité-fonctionnement des écosystèmes. Enfin, nous quantifions l'importance relative des changements du climat, des propriétés physico-chimiques du sol et des communautés plantes et des organismes du sol pour trois fonctions écosystémiques et la multifonctionnalité parallèlement.

Ce chapitre est présenté en anglais, et a fait l'objet d'une publication dans *Functional Ecology*.








Chapitre 1,
Multi-trophic β -diversity mediates the
effect of environmental gradients on the
turnover of multiple ecosystem functions



Intense soil sampling on an elevational gradient.

RESEARCH ARTICLE

Multi-trophic β -diversity mediates the effect of environmental gradients on the turnover of multiple ecosystem functions

Camille Martinez-Almoyna¹  | Wilfried Thuiller¹  | Loïc Chalmandrier²  |
 Marc Ohlmann¹  | Arnaud Foulquier¹  | Jean-Christophe Clément³  |
 Lucie Zinger⁴  | Tamara Münkemüller¹ 

¹CNRS, LECA, Laboratoire d'Ecologie Alpine, Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, Grenoble, France

²Department of Botany, University of Wyoming, Laramie, Wyoming, USA

³CARTELE, UMR 0042 Univ. Savoie Mont Blanc – INRA, Le Bourget-du-Lac, France

⁴Ecole Normale Supérieure, CNRS, Inserm, Institut de Biologie de l'Ecole Normale Supérieure (IBENS), PSL Research University, Paris, France

Correspondence

Camille Martinez-Almoyna
 Email: cmartinezalm@gmail.com

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Abstract

1. Much effort has been devoted to better understanding the effects of environment and biodiversity on ecosystem functioning. However, few studies have moved beyond measuring biodiversity as species richness of a single group and/or focusing on a single ecosystem function. While there is a growing recognition that along environmental gradients, the compositional turnover of multiple trophic groups influences not only productivity but multiple ecosystem functions, we do not know yet which components of multi-trophic β -diversity influence which ecosystem functions.
2. Here, we captured the biodiversity found in soils using environmental DNA to study total soil multi-trophic β -diversity (between all taxa regardless of their trophic group association), horizontal β -diversities (β -diversities within trophic groups) and vertical β -diversity (β -diversity across trophic groups) along a 1,000 m elevational gradient in the French Alps. Using path analyses, we quantified how these β -diversity components mediate the effects of environmental turnover on the turnover of multiple ecosystem functions (i.e. productivity, N-cycling, N-leaching) and overall multifunctionality.
3. While we found a strong direct effect of soil properties on the turnover of multiple ecosystem functions, we also found an indirect effect of climate and soil properties through multi-trophic β -diversity. More specifically, only total multi-trophic β -diversity and the horizontal β -diversity of saprophytic fungi were strongly related to the turnover of multifunctionality and, to a lower extent, the turnover of productivity and N-cycling. Our results suggest that decomposition processes and resulting nutrient availability are key to understand how ecosystem functions change along soil properties and climatic gradients in alpine ecosystems.
4. By demonstrating how saprophytic fungi and their associated trophic groups can offset the direct responses of multiple ecosystem functions to environmental change, our study highlights the paramount importance of multi-trophic diversity for better understanding ecosystem multifunctionality in a changing world.

KEYWORDS

alpine systems, biodiversity–ecosystem functioning, elevation gradient, multi-trophic, path analyses, β -diversity

1 | INTRODUCTION

The idea that biodiversity enhances ecosystem functioning and acts as a buffer against environmental changes is now a consensus in ecology (Cardinale et al., 2012; Hooper et al., 2005). Indeed, diverse communities exploit a wide range of available resources (complementarity effect) and often host the best performing species (selection effect, Hines et al., 2015; Loreau et al., 2001), which ultimately leads to enhanced ecosystem functioning (Bradford et al., 2014; Hector & Bagchi, 2007). This idea mostly comes from studies focusing on diversity within single trophic levels, single ecosystem functions (mainly productivity), and often carried out under controlled conditions (Cardinale et al., 2012; Loreau, 2010). However, understanding how environmental changes across space and time will affect natural ecosystems requires to consider the multiple trophic levels in natural communities and the various ecosystem functions carried out by multi-trophic diversity (Brose & Hillebrand, 2016; Mayor et al., 2017; Soliveres et al., 2016).

Environmental conditions such as climate, available carbon or nitrogen vary by nature over space and time, for example along elevational gradients (Körner, 2003). They directly influence ecosystem functions such as litter decomposition, N-cycling and primary productivity by regulating the rates of bio-chemical processes (Sveinbjörnsson, Abadie, & Butler, 1995). These environmental conditions also select specific plant and soil assemblages, and there is increasing recognition that the taxonomic and functional composition of these species assemblages will then influence the ecosystem functions as well (Hautier et al., 2018; Mori, Isbell, & Seidl, 2018; van der Plas et al., 2016). It has been recently highlighted that a better process-level understanding of the roles and functions of biodiversity may be gained through the study of the turnover of ecological communities, that is their β -diversity, a so far largely underexplored facet of biodiversity (Mori et al., 2018). Therefore, here we aim at deciphering direct and indirect effects of the environment by jointly considering the turnover of environmental conditions, ecosystem functions and β -diversity (van der Plas et al., 2016).

Moreover, recent studies have highlighted the importance of accounting for multi-trophic communities to fully understand the role of β -diversity in ecosystem functions (Hines et al., 2015; Soliveres et al., 2016). Even if experimental work has identified effects at single trophic levels and for single ecosystem functions (Hines et al., 2015), these effects are likely to be more complex in natural systems. Indeed, the effects of different groups of species (same trophic level and/or similar functional characteristics, called trophic groups hereafter) can be simply additive, show synergies or go in different directions (Hines et al., 2015). For example, symbiotic fungi and herbivorous nematodes can have opposite effects on the biomass production of individual plant species (Brussaard, 1998). Therefore, teasing apart the effects of plant, symbiotic fungi and herbivorous nematodes diversity on ecosystem functioning requires a multi-trophic approach. Recently, Soliveres et al. (2016) showed that the richness variation of three trophic groups needs to be known to properly explain a single ecosystem function. In addition, depending on the

amount of functional redundancy between trophic groups, their relative importance may change along environmental gradients (Setälä, Berg, & Jones, 2005). In other words, expanding the traditional focus on horizontal β -diversity (i.e. within a single trophic group) to a vertical perspective of multi-trophic β -diversity (i.e. variation across trophic groups) and a total multi-trophic β -diversity (i.e. of all taxa regardless of their trophic group) should critically improve our understanding of the role of multi-trophic β -diversity on ecosystem functioning (Figure 1).

Finally, natural ecosystems are characterized by many interconnected ecosystem functions. It is likely that distinct ecosystem functions respond differently to various components of multi-trophic β -diversity. A changing environmental context may also alter the links between ecosystem functions and multi-trophic β -diversity (Bradford et al., 2014; Setälä et al., 2005). The influence of horizontal and vertical β -diversities on ecosystem functioning could thus be mis-quantified when focusing on a single function, for example primary productivity, as a proxy for overall ecosystem functioning (Hector & Bagchi, 2007). Indeed, whereas turnover of productivity may be driven by the horizontal β -diversities of plants and fungi, turnover of nutrients may depend more on the horizontal β -diversity of bacteria (Moore et al., 2004; Wall et al., 2012). The turnover of N-leaching, usually more related to abiotic characteristics of the ecosystem, might instead be independent of multi-trophic β -diversity. Thus, studying horizontal and vertical β -diversity effects on different ecosystem functions should clarify how multifunctionality along environmental gradients is driven by different trophic groups (Delgado-Baquerizo et al., 2016).

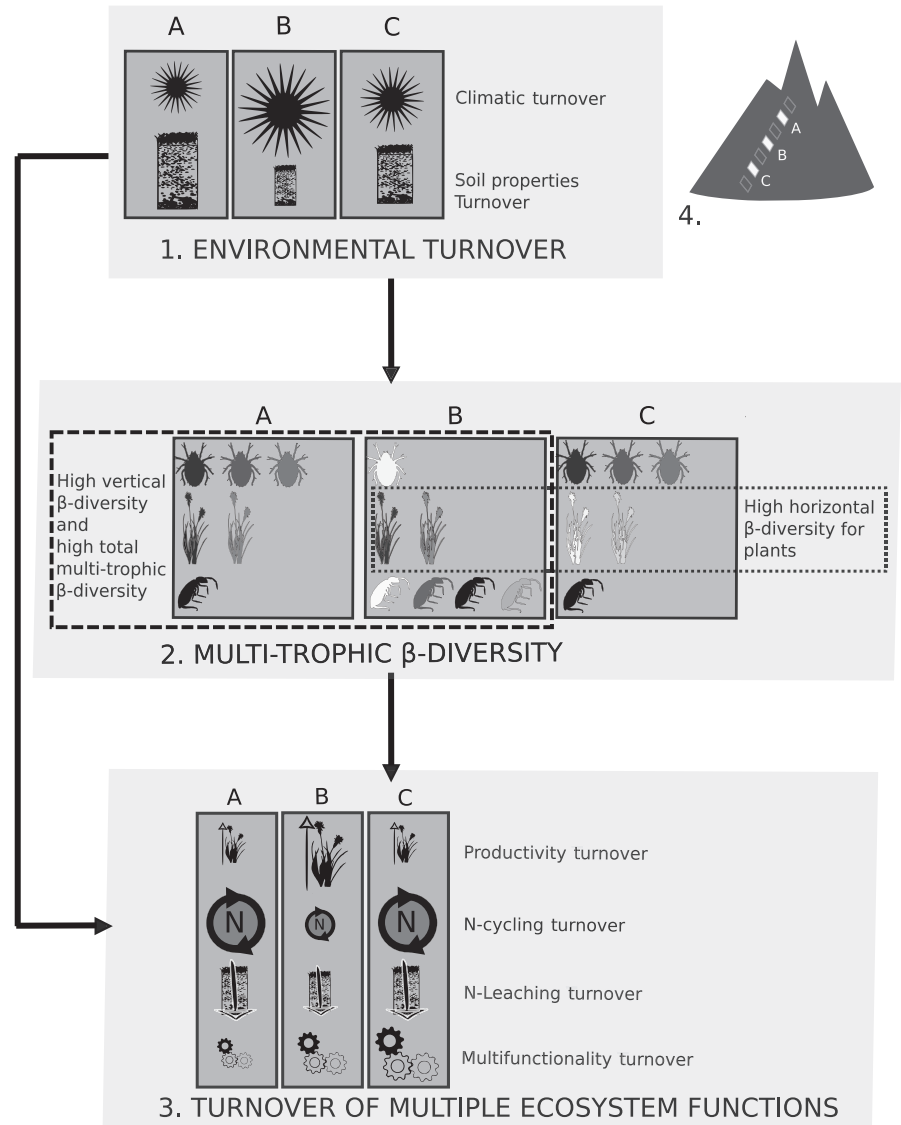
Here, we study the direct and indirect effects of environmental turnover on the turnover of multiple ecosystem functions in mountain grasslands by explicitly considering the role of soil horizontal and vertical β -diversities (Figure 1). Along a 1,000 m elevation gradient, we surveyed climate and soil properties, multi-trophic biodiversity of the most important trophic groups of the plant-soil compartment (as inferred from environmental DNA, Kress, García-Robledo, Uriarte, & Erickson, 2015; Taberlet, Coissac, Hajibabaei, & Rieseberg, 2012) and several in situ ecosystem processes (i.e. primary productivity, N-leaching, N-cycling and multifunctionality). We first tested how total multi-trophic β -diversity mediates the effects of environmental turnover on turnover of multiple ecosystem functions and whether these effects varied between ecosystem functions. Second, we tested the independent effects of vertical multi-trophic β -diversity and horizontal β -diversities on the spatial turnover of multiple ecosystem functions. Finally, we jointly analysed the relative contributions of horizontal β -diversities of different trophic groups to the spatial turnover of multiple ecosystem functions.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was carried out in the French Alps, along a continuous elevation gradient (1,750–2,725 m, Arves Massif, 45.12°N, 6.40°E)

FIGURE 1 Environmental turnover (box 1) affects turnover of multiple ecosystem functions (box 3) directly and indirectly through multi-trophic β -diversity (box 2) along a 1,000 m elevation gradient (box 4). In our example (turnover between plots A, B and C, boxes 2 and 4), total multi-trophic β -diversity is high between A and B but low between A and C; horizontal β -diversity is high between A and B for mites and between A and C for plants but low between B and C for springtails (community C is nested in B); vertical β -diversity (variation of MOTUs richness across the groups) is high between B and C but low between A and C



in a cow-grazed pasture. Subalpine grasslands dominate the bottom of the gradient while sparsely vegetated alpine meadows characterize higher elevations. Ten sites were sampled in summer 2012 along the same south-facing slope, and they were separated by an 100 m elevation difference and an average distance of 340 m. Each site consisted of two 10 m \times 10 m plots with homogeneous vegetation (see Chalmandrier et al., 2017, for more details).

2.2 | Environmental variables

We considered four bioclimatic variables known to be strong drivers of community assembly in mountain systems (Körner, 2003): soil temperature, solar radiation, growing season length (GSL) and number of frost days. Growing season length and annual number of frost days were derived from Landsat 7 and 8 imageries (Carlson, Choler, Renaud, Dedieu, & Thuiller, 2015). Solar radiations were calculated with the area solar radiation tool in ArcGIS (version 10.2, 2013; Redlands, CA, USA) using a 2-m LiDAR digital elevation model and the clear sky model set to a sky

size of 2,800 pixels (Carlson et al., 2015). Soil temperature was measured in the field.

To capture small-scale variation, we added local topographic variation using elevation, slope, the topographic wetness index (TWI) and the topographic position index (TPI) with a 50 cm resolution digital elevation model derived from the airborne LiDAR data acquired the year of sampling.

Finally, we measured soil properties from three soil cores (10 cm depth, 5 cm diameter) taken in a 1.25 m \times 1.25 m subplot at the centre of each plot. Two soil cores were weighed, 5 mm sieved and pooled for quantifying soil moisture, soil organic matter content, pH, soil texture using standard protocols (Robertson, Coleman, Sollins, & Bledsoe, 1999), and total soil N and C content using an elemental analyzer (FlashEA1112, Thermo Fisher Scientific). We added 100 ml of distilled water to saturate the third soil core and calculate the water-filled pore space (WFPS). The soil core was then air-dried, sieved and grounded to calculate gravel weight, total porosity and apparent density (Legay et al., 2014).

We found that the first two axes of a principal component analyses run for all produced (and normalized) environmental variables

(Figure S1) captured, respectively, 48.1% and 19.4% of the environmental variability. We then split the environmental variables in two groups corresponding to the major environmental gradients of the study area: a climatic gradient and a gradient of soil properties.

2.2.1 | Climate

To measure the turnover of climate (and topography), we focused on the set of environmental variables that load strongest on the first axis of the PCA: solar radiation, soil temperature, mean and variance of GSL, number of frost days, percentage of WFPS, TPI, TWI, altitude and slope. We then computed Euclidean distances between each pair of plots for these environmental variables and defined these pairwise distances as a measure of *climatic turnover*.

2.2.2 | Soil properties

To measure the turnover of soil properties, we focused on the set of environmental variables that load strongest on the second axis of the PCA: gravel mass, apparent density, soil porosity, soil pH, percentage of organic matter and of total N. We then computed Euclidean distances between each pair of plots for these environmental variables and defined these pairwise distances as a measure of *soil properties turnover*.

2.3 | Multi-trophic data

2.3.1 | Sampling

To get an estimate of the diversity found in each of the sampled plot, we analysed soils samples through DNA metabarcoding. In each plot, we collected 21 soil samples (10 cm depth, 5 cm diameter) to account for small-scale heterogeneity (ten samples on each diagonal and a supplementary central one). Soil biodiversity was measured with four different DNA markers. Two universal markers, one amplifying all eukaryotes (v6-v7 region of the 18S rRNA gene) and one amplifying all bacteria (v5-v6 region of the 16S rRNA gene), were used to obtain a general overview of the soil multi-trophic composition of the plots. We also used two additional markers focused on fungi (internal transcribed spacer 1) and vascular plants (chloroplast trnL-P6 loop). Molecular analyses and data curation are presented in Ohlmann et al. (2018). We pooled the 21 samples per plot to obtain a single community of molecular taxonomic units (MOTUs) per plot and converted the data into presence-absences. The curated sequencing data as well as associated metadata are available on the Dryad Digital Repository under accession <https://doi.org/10.5061/dryad.5b58400>.

2.3.2 | Definition of the trophic groups

Following Ohlmann et al. (2018), we grouped the MOTUs based on their taxonomic affiliation, shared trophic resources and main

functions, such as organic matter decomposition. Hereafter, we will refer to them as *trophic groups*, while other definitions like trophic guilds or tropho-functional groups could have been given.

We first assigned all vascular plant MOTUs to a single trophic group of primary producers, which directly contribute to ecosystem productivity and to the quality of litter inputs to soils with potential impacts on nitrogen cycling and loss (Hooper & Vitousek, 1998). Second, we considered microbial MOTUs (i.e. bacteria and fungi) as decomposers. We distinguished bacteria from fungi since their metabolic functions do not fully overlap (De Boer, Folman, Summerbell, & Boddy, 2005). We further used the FUNguild database (Nguyen et al., 2016) distinguish symbiotic (i.e. mycorrhizal), saprophytic and pathogenic fungi. Finally, the diversity of soil micro- and meso-fauna regulates the activity and abundance of soil microbes and associated nutrient recycling by shredding/grazing leaf litter or feeding directly on microbes (Crowther et al., 2015; Puleman et al., 2012). They should thus shape the multi-trophic β -diversity and have a determinant impact on multiple ecosystem functions. We thus extracted from the eukaryotes marker, all MOTUs assigned to nematodes, springtails and oribatid mites which are the most abundant below-ground multicellular organisms (Wall et al., 2012). We further distinguished bacterivore from herbivore/fungivore nematodes using the NEMguild database (Nguyen et al., 2016), where nematode species trophic modes are defined on the basis of the morphology of their mouth.

2.3.3 | Different components of multi-trophic β -diversity

First, we computed the true turnover (Baselga, 2010) of the whole soil community (i.e. ignoring trophic groups) as a measure of the *total multi-trophic β -diversity* using the Simpson dissimilarity index between each pair of plots (Equation 1).

$$\beta_{kl} = \frac{\min(\|P_k\| - \|P_k \cdot P_l\|, \|P_l\| - \|P_k \cdot P_l\|)}{\|P_k \cdot P_l\| + \min(\|P_k\| - \|P_k \cdot P_l\|, \|P_l\| - \|P_k \cdot P_l\|)} \quad (1)$$

where k and l are the focal plots (such as $1 \leq k \leq K \wedge 1 \leq l \leq K$, K the total number of plots), $P = (P_{ki})_{\substack{1 \leq k \leq K \\ 1 \leq i \leq n}}$ is the community matrix of the whole soil community (n is the total number of MOTUs and $P_{ki} \in \{0,1\}$ denotes the presence of the MOTU i in plot k). P_k is the community vector of the plot k and $\|P_k\| = \sum_{i=1}^n P_{ki}$ denotes the MOTUs richness of the plot k . $\|P_k \cdot P_l\|$ is the number of shared MOTUs between plot k and l .

Second, we calculated the true turnover (Baselga, 2010) of each single trophic group as measures of *their horizontal β -diversities* using the Simpson dissimilarity index between each pair of plots (Equation 2).

$$\beta_{kl}^g = \frac{\min(\|P_k^g\| - \|P_k^g \cdot P_l^g\|, \|P_l^g\| - \|P_k^g \cdot P_l^g\|)}{\|P_k^g \cdot P_l^g\| + \min(\|P_k^g\| - \|P_k^g \cdot P_l^g\|, \|P_l^g\| - \|P_k^g \cdot P_l^g\|)} \quad (2)$$

where k and l are the focal plots (such as $1 \leq k \leq K \wedge 1 \leq l \leq K$, K the total number of plots), g is the focal trophic group, $P_{ki}^g = (P_{ki}^g)_{\substack{1 \leq k \leq K \\ 1 \leq i \leq n_g}}$ is the community matrix of the group g (n_g is the total number of MOTUs, and $P_{ki}^g \in \{0,1\}$ denotes the presence of the MOTU i in plot k). P_{nk}^g is the community vector (of the group g) of the plot k , and $\|P_{nk}^g\| = \sum_{i=1}^{n_g} P_{ki}^g$ denotes the richness of the plot k for the group g .

And finally, we calculated the richness variation across trophic groups as a measure of the vertical β -diversity using the Bray–Curtis (BC) dissimilarity index between each pair of plots (Legendre & Legendre, 1998):

$$BC \beta_{kl} = \frac{2 \sum_{g=1}^G \min(\|P_{nk}^g\|, \|P_{nl}^g\|)}{\sum_{g=1}^G (\|P_{nk}^g\| + \|P_{nl}^g\|)} \quad (3)$$

where G is the total number of trophic groups.

2.4 | Multifunctionality data

2.4.1 | Productivity

We measured turnover of primary productivity using two types of data. First, we measured the total green biomass of the year in situ, which constitutes a good proxy of the annual biomass increment. We harvested all the vegetation at the ground level on a $1 \text{ m} \times 1 \text{ m}$ plot, sorted out the current year live and recently senescent material, dried and weighed it. We used the spatial mean and variability of the Normalized Difference Vegetation Index (NDVI), a proxy of the photosynthetic activity (Yoder & Waring, 1994), as a complementary measure. For each plot, we computed spatial mean and variance of NDVI using an airborne 15 cm resolution infrared picture taken at the productivity peak in August 2012 (Yoder & Waring, 1994) for the whole elevation gradient. We then calculated their Euclidean distance for each pair of plots. *Productivity turnover* was then defined as the Euclidean distances between each pair of plots for the three measures: total green biomass, spatial mean and variance of NDVI.

2.4.2 | N-cycling

To estimate turnover of N-cycling, we used the same two soil cores as for soil physico-chemical measurements (see environmental data). We estimated the decomposability of organic matter by calculating the C:N ratio. Soil nutrients (nitrate (NO_3^-), ammonium (NH_4^+), total dissolved nitrogen (TDN) and dissolved organic nitrogen (DON) were determined from soil extracts with $0.5 \text{ M K}_2\text{SO}_4$ (Jones & Willett, 2006) using a photometric analyzer (Gallery Plus, Thermo Fisher Scientific). We estimated the relative availability of different forms of N by calculating the ratio of total dissolved nitrogen on total nitrogen (N-TDN/N) and the ratio of dissolved organic nitrogen on mineral nitrogen (N-DON/(N- NO_3^- + N- NH_4^+)) because dissolved organic N, particularly amino acids, constitutes a large

portion of the N budget of plants in these high latitude ecosystems (Loomis, Ruess, Sveinbjörnsson, & Kielland, 2006). Finally, potential nitrogen mineralization rates were used to estimate the ability of the ecosystem to mobilize soil organic matter and supply mineral N (Legay et al., 2016), and measured based on anaerobic incubations of fresh soil subsamples (dark, 7 days, 40°C), during which organic N was mineralized and accumulated as NH_4^+ (Waring & Bremner, 1964; Wienhold, 2007). The difference between NH_4^+ contents in a given sample before (t_1) and after the anaerobic incubation (t_2) gave $\text{PNM} = [(\text{NH}_4^+ \text{ at } t_2) - (\text{NH}_4^+ \text{ at } t_1)] / \text{dw} / 7 \text{ days}$. *N-cycling turnover* was then defined as the Euclidean distance between each pair of plots for C/N, N-TDN/N, potential mineralization and N-DON/(N- NO_3^- + N- NH_4^+).

2.4.3 | N-leaching

As a proxy for nitrogen losses through leaching, we measured potential ammonium and nitrate leaching from the percolate. Percolated water was filtered through a Whatman filter paper $n^\circ 42$ ($2.5 \mu\text{m}$ pore size) and analysed using a photometric analyzer to calculate potentially leached $\text{NH}_4^+ \text{-N}$ and $\text{NO}_3^- \text{-N}$ (Legay et al., 2016). *N-leaching turnover* was then defined as the Euclidean distance between each pair of plots for potential ammonium and nitrate leaching.

2.4.4 | Multifunctionality

We calculated *multifunctionality turnover* as the Euclidean distance between each pair of plots for all measured ecosystem processes. Correlations of each ecosystem function to the multifunctionality turnover are presented in Appendix (Figure S2). We also run all the analyses for each ecosystem process separately.

2.5 | Statistical analyses

To address our first two objectives, we performed a set of path analyses using the lavaan package in R (Figure 2; R Core Team, 2018; Rosseel, 2012). All variables were first centred and normalized. First, we built four path analyses independently for each of the three single ecosystem functions and multifunctionality to determine the effects of climatic and soil properties turnover and of total multi-trophic β -diversity. Second, we built four path analyses independently for each of the three single ecosystem functions and multifunctionality to determine the effects of environmental turnover (turnover of climate and soil properties) and of vertical β -diversity. Finally, we built 36 independent path analyses independently to assess the effect of each of the 9 trophic groups on each of the three single ecosystem functions and multifunctionality while including in each model the effects of the two sets of variables (climate and soil properties) for environmental turnover.

To address our final objective, we built an integrated path model for each ecosystem function and multifunctionality. We selected variables in a semi-exploratory way. We always included climatic and

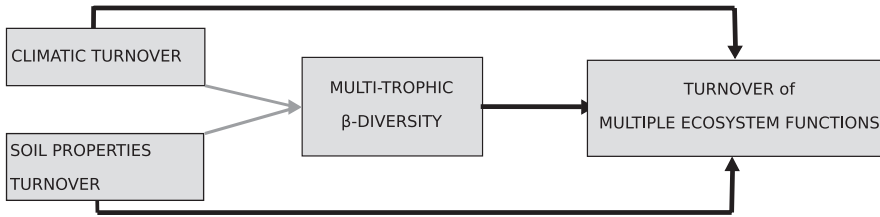


FIGURE 2 Structure of the tested path models

soil properties turnover to account for their direct effects on both biodiversity and ecosystem functions. In respect to multi-trophic β -diversity, we only included the trophic groups that had a significant horizontal effect and estimated their direct effects on turnover of multiple ecosystem functions. Since we did not have any prior expectation on their causal relationships, we did not specify any directional link between them. However, we let free covariances between each pair of trophic groups to account for the effect of their probable interactions. In turn, all our path analyses were saturated and we thus could not test the structure of the models.

For all above-mentioned path analyses, we tested for the significance of the effects using a parametric bootstrap procedure based on 10,000 sampling with simultaneous replacement of rows and columns to quantify confidence intervals for the parameters (Fourtune et al., 2018). This approach is suitable when modelling pairwise distances where the elements of one row/column are not independent of each other (Fourtune et al., 2018). Parameters are significant when the confidence intervals do not include zero.

3 | RESULTS

Turnover in soil properties was a consistent and strong direct predictor of multifunctionality and of the three ecosystem functions, while climatic turnover was not (Figures 3 and 4). Total multi-trophic β -diversity was a significant predictor of productivity and multifunctionality turnover and almost as important as soil properties turnover. However, it did not explain N-cycling and N-leaching turnover (Figure 3).

In contrast, when using vertical β -diversity instead of total multi-trophic β -diversity, the diversity effect vanished and only soil properties turnover had a significant effect on turnover of ecosystem functions, including multifunctionality (Figure 4). In other words, the effect of total multi-trophic β -diversity on turnover of multiple ecosystem functions was not driven by vertical β -diversity.

Finally, focusing on the independent effects of horizontal β -diversities of the different trophic groups, the most important

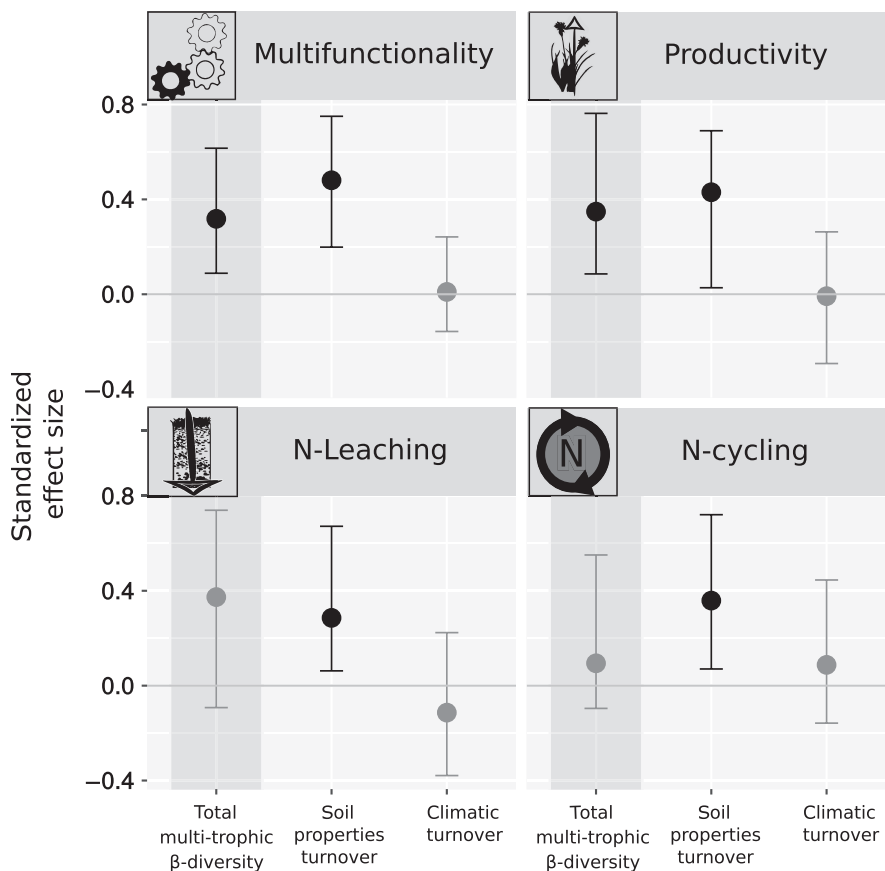
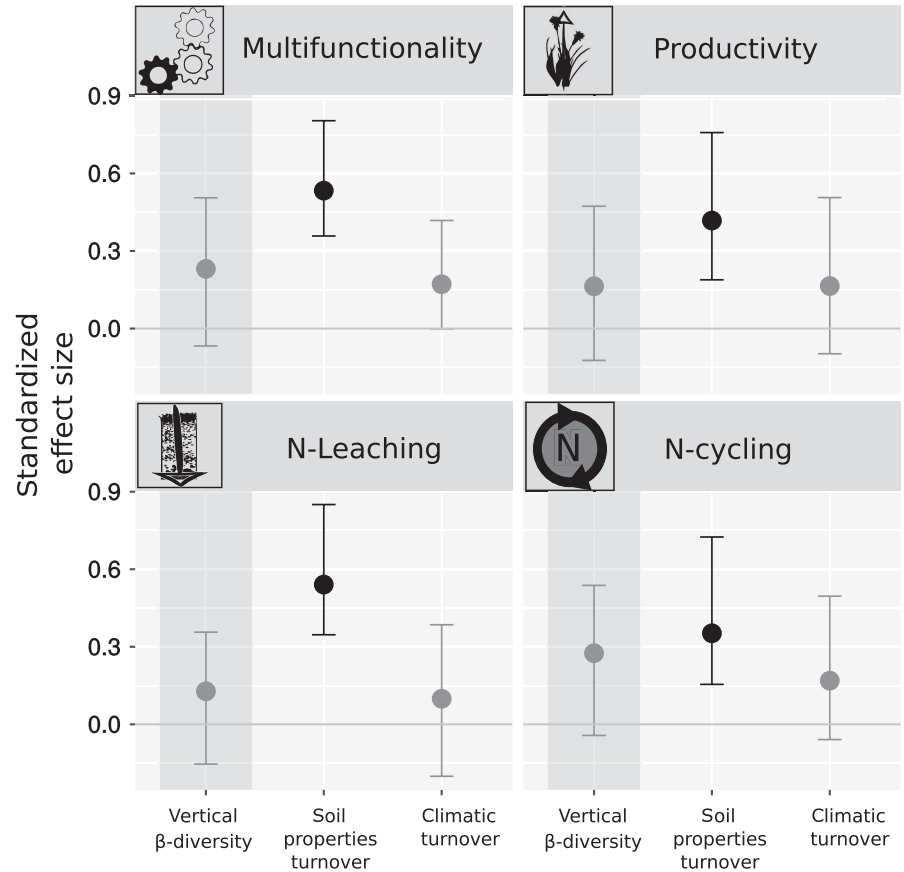


FIGURE 3 Total multi-trophic β -diversity mediates the effect of environmental turnover on the turnover of multiple ecosystem functions. Only direct standardized effects are represented. Direct standardized effect of total multi-trophic β -diversity is highlighted with a grey area. Significant and non-significant standardized effects are represented with black and grey points and their associated confidence intervals, respectively. Direct standardized effects of climatic and soil turnover on the total β -diversity are represented in appendix (Figure S6)

FIGURE 4 Vertical β -diversity does not mediate the environmental turnover effect on the turnover of multiple ecosystem functions. Only direct standardized effects are represented. Direct standardized effect of vertical β -diversity is highlighted with a grey area. Significant and non-significant standardized effects are represented with black and grey points and their associated confidence intervals, respectively. Direct standardized effects of climatic and soil turnover on the vertical β -diversity are represented in Figure S6



predictors of multifunctionality and productivity turnover were soil properties turnover and horizontal β -diversities of saprophytic fungi, followed by symbiotic fungi, herbi-fungivore nematodes, pathogenic fungi and bacteria (Figure 5; Figure S3). For N-cycling turnover, the most important predictors were soil properties turnover and horizontal β -diversities of saprophytic fungi, followed by symbiotic fungi and pathogenic fungi (Figure 5; Figure S3). No component of multi-trophic β -diversity was linked to N-leaching turnover (Figure 5), for which soil properties turnover was the only significant predictor (Figure S3). For the non-aggregated ecosystem processes, different subsets of trophic groups were the best predictors, but the general trends remained (Figure S7).

The integrated path models that considered several trophic groups together, but were built independently for each ecosystem function and multifunctionality, suggested how the pieces of the puzzle can be put together (Figure 6). Consistent with the results above, soil properties were of primary importance for all considered ecosystem functions and multifunctionality directly, whereas climate was not (Figure 6; Figures S4 and S5). Similar figures emerged when considering each ecosystem process independently (Figure S7).

Climatic turnover and soil properties turnover influenced horizontal β -diversities of most of the trophic groups (Figure S6). Pathogenic fungi (Figure 6; Figures S4 and S5; Table S1) and, to a lower extent, saprophytic fungi (Table S1) were directly affected by climate. Bacteria and, to a lesser extent, herbi-fungivorous

nematodes and saprophytic fungi were directly affected by soil properties (Figure 6; Figures S4 and S5; Table S1).

Importantly, all trophic groups were interlinked and were thus involved in the indirect effects of climate and soil properties on multiple ecosystem functions. Pathogenic fungi were strongly linked to symbiotic and saprophytic fungi (Figure 6; Figures S4 and S5). Bacteria were linked especially to saprophytic fungi (Figure 6; Figure S4) and to a lesser extent to symbiotic fungi (Table S1).

Finally, the only significant biotic predictor for the turnover of multifunctionality was the horizontal β -diversity of saprophytic fungi (Figure 6). Additionally, horizontal β -diversity of herbi-fungivorous nematodes showed a strong effect even if not significant (Table S1). Results for productivity turnover showed comparable trends but with weaker effects (Figure S4). The combined horizontal β -diversities did not explain N-cycling turnover (Figure S5). N-leaching turnover was not considered here since it was not positively linked to any of the multi-trophic β -diversity components in the previous path analyses. When we considered the non-aggregated ecosystem processes in the same way, different trophic groups, also mostly fungi, had a significant effect on different ecosystem processes: saprotroph fungi on dissolved N:total N, symbiotic fungi on soil C:N, pathogenic on dissolved organic N:dissolved inorganic N and fungi-herbivorous nematodes on total green biomass (Figures S7c,d).

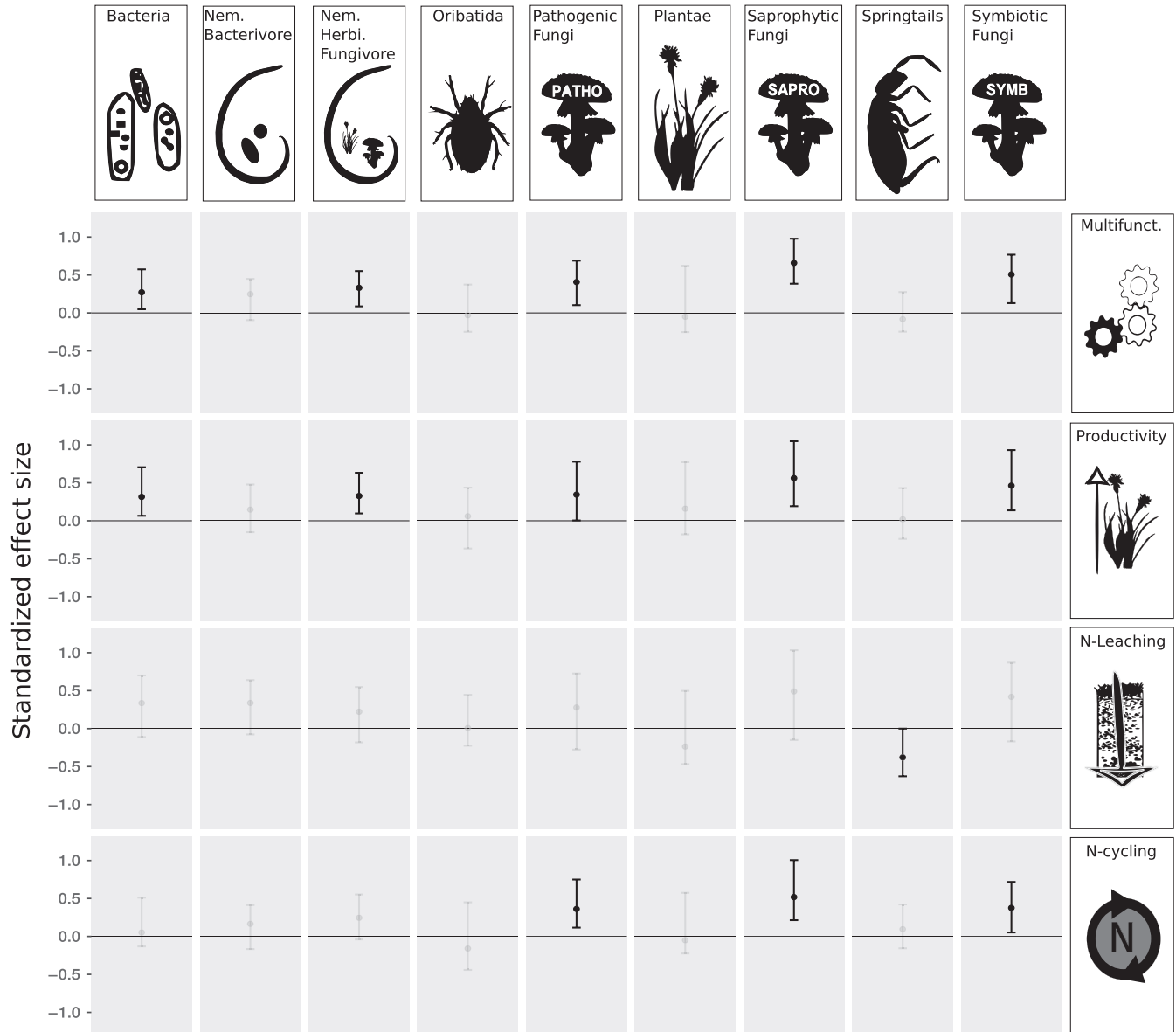


FIGURE 5 Horizontal β -diversities of several trophic groups mediate the environmental turnover effect on the turnover of multiple ecosystem functions. Only direct standardized effects are represented. Significant and non-significant standardized effects are represented with black and grey points and intervals, respectively. Direct standardized effects of climatic and soil turnover on the horizontal β -diversities and on the multiple ecosystem functions are in Figures S6 and S3, respectively

4 | DISCUSSION

Brose and Hillebrand (2016) recently called for a shift from traditional biodiversity and ecosystem functioning experiments under controlled conditions to natural systems with (a) multi-trophic communities, (b) varying environmental conditions and (c) larger spatial scales. Here, we tackled this challenge by using multi-trophic β -diversity measures to investigate how they mediate the influence of environmental turnover on the turnover of multiple ecosystem functions.

In our study along an elevation gradient in the French Alps, we found that environmental turnover influenced ecosystem functioning turnover both directly and indirectly via biodiversity turnover.

Surprisingly, only the turnover of soil but not climatic properties contributed significantly to the direct pathway. Due to varying limitations in soil organic matter and water availability, decomposition rates and nutrient retention times changed across the gradient, with direct consequences on N-cycling, productivity and N-leaching (Gavazov, 2010; Louca et al., 2018). In contrast to our findings, a large body of literature on size reduction of alpine plants with increasing elevation led us expect that differences in temperature-related variables (e.g. GSL, number of frost days and solar radiations) captured in our climatic turnover variable (PCA axis 1, Figure S1) would drive at least productivity turnover (Choler, 2005; Körner, 2003; Schöb, Kammer, Choler, & Veit, 2009; Sundqvist, Sanders, &

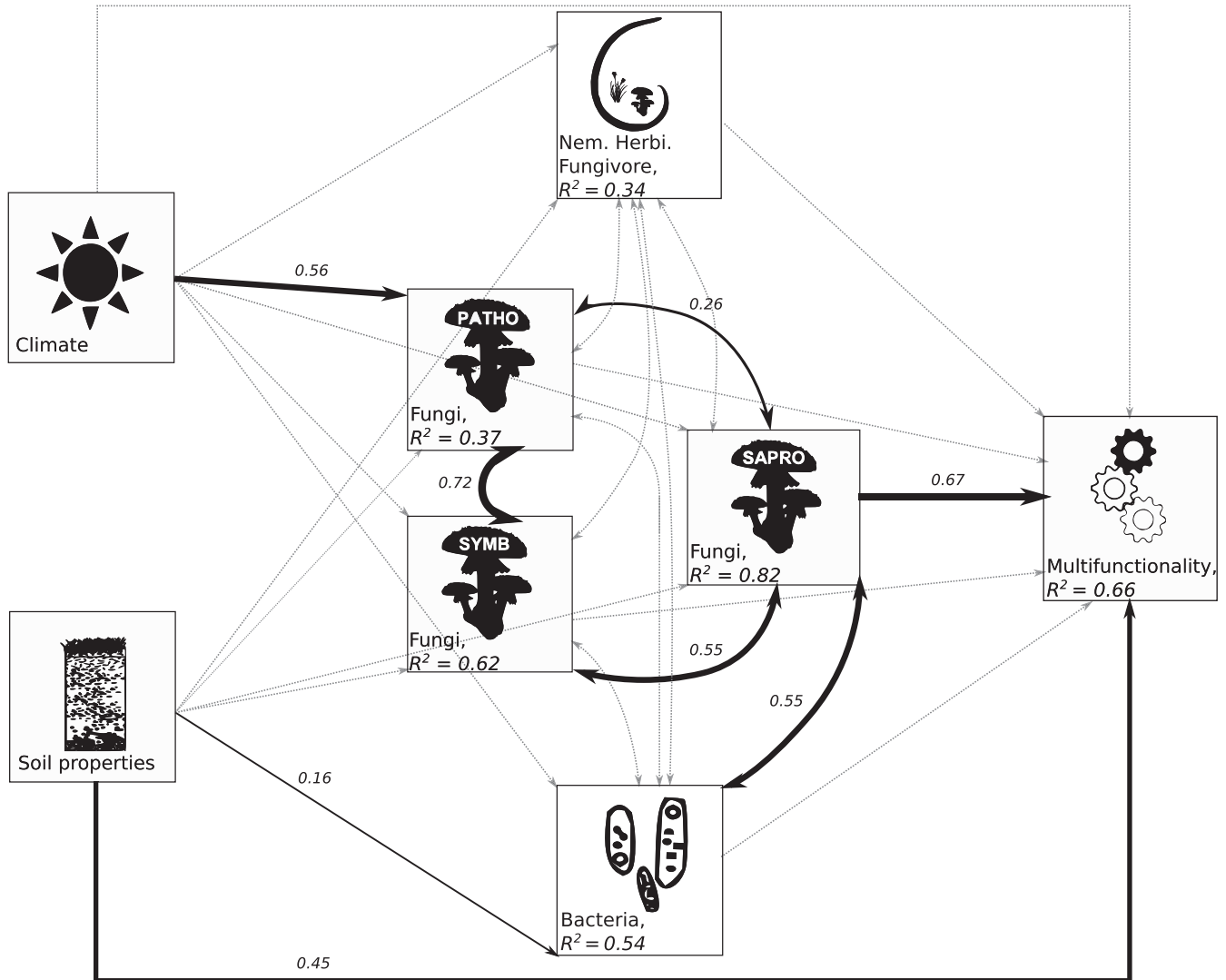


FIGURE 6 Integrated path model highlighting the direct and indirect effects of climate and soil properties turnover on turnover of ecosystem multifunctionality. The size of the arrows is proportional to the size of the associated standardized path coefficients (only for significant paths). Dotted grey lines represent non-significant paths. Paths with double arrows represent correlations

Wardle, 2013). However, a few recent studies that also included the indirect effect of climate through biodiversity support our results. Together, this suggests that under natural conditions, the direct effect of climate on ecosystem functioning can be overridden and/or compensated by complex cascading effects from micro-organisms to plants. For example, Crowther et al. (2015) showed that turnover of ecosystem functions can be bottom-up regulated by the climatic conditions in harsh environments but top-down regulated through consumption of the microbes by the soil fauna, when environmental constraints are less extreme. Also, at the global scale, Delgado-Baquerizo et al. (2016) reported only a negligible effect of temperature on multifunctionality, while the effect of microbial community diversity was always strong and positive. Our results also demonstrated that on top of its direct response to soil properties, turnover of multiple ecosystem functions depends on soil and climatic turnovers through their effects on the β -diversities of several trophic groups (Figure S6).

In order to untangle these cascading effects, we contrasted the effects of several multi-trophic α - and β -diversity aspects on multiple ecosystem functions. Unlike total β -diversity (Figure 3), total α -diversity (Figure S8) appeared to be a weak predictor of ecosystem functioning, suggesting that a number of species perform similar functions in soil communities, that is they are functionally redundant. Also, vertical β -diversity did not cause turnover of ecosystem functions (Figure 4), indicating that whatever their richness, trophic groups cluster particularly functionally redundant species (Louca et al., 2018; Setälä et al., 2005). Nevertheless, intra-group functional redundancy level may depend on the studied trophic group. For example, Mori et al. (2016) argue that changes in the composition of fungal communities can modify ecosystem functioning by altering which ecosystem functions are preferentially provided, while Louca et al. (2018) showed that bacterial taxa have similar broad metabolic potential, leading most ecosystem functions to be barely dependent on the taxonomic composition of bacterial communities. Likewise, in our study, the relationship

between α -diversity and ecosystem functions was linear and positive only for a small selection of trophic groups and ecosystem functions (Figure S8). Together, these results suggest that a few of our trophic groups contain functionally complementary species, pivotal for ecosystem functioning.

To avoid an overestimation of the direct effect of these key trophic groups on ecosystem functioning (Ohlmann et al., 2018), the horizontal β -diversities of their interaction partners partaking in the studied ecosystem functions should not be omitted (Brose & Hillebrand, 2016; Hines et al., 2015; Thompson et al., 2012). As such, we found that most trophic groups influenced ecosystem functions when considered alone (Figure 5; Figure S6). However, when the horizontal β -diversities of their interaction partners were added, only the saprophytic fungi β -diversity was significantly linked to the turnover of multifunctionality, and to a lesser extent to productivity and N-cycling (Figure 6; Figures S4 and S5; Table S1). Saprophytic fungi are critical in the decomposition process because they produce exo-enzymes processing complex organic compounds (Baptist et al., 2008; Moore et al., 2004; Wall et al., 2012). The resulting simpler compounds, scarce in alpine environments, become available for plant and microbial absorption (Moore et al., 2004; Wall et al., 2012). Changes in saprophytic fungi communities should thus alter nutrient availability, which impacts productivity, N-cycling and multifunctionality (Mori et al., 2016; Valencia et al., 2018). Nevertheless, also the other trophic groups β -diversities indirectly drove ecosystem functions turnover through their strong links to the saprophytic fungi β -diversity. In line with a growing number of studies, this suggests that species links in soil food webs could be pivotal for ecosystem functioning and that they need to be accounted for in addition to just the β -diversity of species within (horizontal) and across (vertical) trophic groups (Ohlmann et al., 2019; Setälä et al., 2005; Thompson et al., 2012). In particular, we found that specific regulators of fungi (e.g. herbi-fungivorous nematodes, Figure 6; Figure S4) and competitors (e.g. bacteria and other fungal trophic groups, De Boer et al., 2005; Nazir, Warmink, Boersma, & Van Elsas, 2010) tend to have an indirect influence on multiple ecosystem functions through their influence on the compositional turnover of saprophytic fungi. In turn, climatic variables and ecosystem functions are not linked by a single indirect pathway but by multiple indirect pathways with saprophytic fungi as a corner stone. This result is in line with several other studies (Mori et al., 2016; Setälä et al., 2005; Valencia et al., 2018).

Our results on both an integrated measure of multifunctionality and more specific measures of three important functions of alpine ecosystems (i.e. productivity, N-cycling, N-leaching, Sundqvist et al., 2013) are also consistent with several studies arguing that major biogeochemical pathways are regulated by a reduced number of energy pathways, broadly supported by some key trophic groups and sometimes strongly driven by some limiting environmental conditions (Louca et al., 2018). At the highest scale of aggregation of multiple ecosystem functions, saprophytic fungi being keystones of multifunctionality suggests that, due to the strong nitrogen limitations in

alpine ecosystems (Loomis et al., 2006; Robson, Lavorel, Clement, & Roux, 2007; Sundqvist et al., 2013; Sveinbjörnsson et al., 1995), decomposition is acting as a bottle neck for other ecosystem functions (Setälä et al., 2005; Wardle, 2002). Indeed, ammonium and nitrate produced by decomposers can be leached out, adsorbed on soil particles, denitrified, volatilized or assimilated by plants and bacteria. The balance between these processes mainly depends on abiotic soil conditions which control water and solute transfers, and on the nitrogen demand of plant and micro-organisms (Robson et al., 2007) especially during the productivity peak when plant N-uptake is the highest (Legay et al., 2016). Therefore, weaker effects of each trophic group horizontal β -diversity on the turnover of productivity and N-cycling could be explained by a functional complementary effect between trophic groups of fungi and their specific biotic regulators, and feedbacks between trophic groups and soil. Adding other, and so far, a bit less studied pathways (e.g. P-cycling, Leff et al., 2015), may have uncovered additional direct and indirect links of environmental turnover and functioning turnover via β -diversities.

To conclude, looking at multiple ecosystem functions showed an important mediating role of multi-trophic β -diversity. Our finding particularly supports the paramount importance of decomposers, especially saprophytic fungi, and of their interaction partners, in nitrogen limited alpine systems. In this sense, our study supports recent calls to explicitly integrate known interactions between trophic groups (Thompson et al., 2012) and for temporal monitoring of the ecosystems (Brose & Hillebrand, 2016), two missing steps towards a better understanding of functional complementarity and selection effects of diversity and of their role in multiple ecosystem functions (Hines et al., 2015) and their trade-offs in natural systems.

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AUTHORS' CONTRIBUTIONS

C.M.-A., T.M. and W.T. conceptualized the overall study and methodology. L.C., J.-C.C., T.M., W.T. and L.Z. collected the data. L.Z. runs the bioinformatic pipelines. M.O. built the trophic groups, and C.M.-A. run all statistical analyses. C.M.-A. led the interpretation of the results and the writing with contributions of all authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.m2579m0> (Martinez Almoyna et al., 2019).

ORCID


Camille Martinez-Almoyna  <https://orcid.org/0000-0002-3624-7932>

Wilfried Thuiller  <https://orcid.org/0000-0002-5388-5274>

Loïc Chalmandrier  <https://orcid.org/0000-0002-2631-0432>

Marc Ohlmann  <https://orcid.org/0000-0003-3772-3969>

Arnaud Foulquier  <https://orcid.org/0000-0002-8308-5841>

Jean-Christophe Clément  <https://orcid.org/0000-0002-0841-7199>

Lucie Zinger  <https://orcid.org/0000-0002-3400-5825>

Tamara Münkemüller  <https://orcid.org/0000-0001-9743-1322>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Du premier chapitre au chapitre 2 (et au reste de la thèse) ...

Dans le premier chapitre, le long d'un seul gradient d'altitude et à l'aide de variables résumées, nous avons étudié l'effet de la variation spatiale du climat et des propriétés physico-chimique du sol sur la communauté de plantes et du sol et sur le fonctionnement de l'écosystème. Nous avons montré que les changements environnementaux (climat et sol) affectent la composition de la plupart des groupes trophiques des plantes et du sol, mais que seules les propriétés physico-chimiques du sol expliquent directement les changements des fonctions écosystémiques et de la multifonctionnalité. Cependant, l'absence du lien entre climat et fonctionnement de l'écosystème est surprenante, notamment en ce qui concerne la productivité primaire, et soulève de nouvelles questions : *Ce résultat persiste-t-il à plus large échelle ? Dans quelle mesure l'effet des différentes variables climatiques et du sol était-il caché par l'utilisation de variables résumées ? Dans quelle mesure l'utilisation de différents gradients d'altitude permettrait-elle de mieux différencier les effets des différentes variables environnementales ?*

Dans ce deuxième chapitre, nous commençons à aborder ces questions en différenciant l'effet de deux variables climatiques essentielles dans les systèmes alpins de celui de deux propriétés physico-chimiques du sol, connues pour être des bons prédicteurs des communautés de plantes et du sol et de leur fonctionnement. Nous irons également plus loin sur ces questions dans un troisième et quatrième chapitre.

De plus, dans le chapitre précédant, nous avons adopté une approche multi-trophique des communautés de plantes et du sol, et comparé la pertinence de la β -diversité multi-trophique totale, horizontale et verticale dans l'étude du lien entre environnement, communauté de plantes et du sol et fonctionnement de l'écosystème. Nous avons montré que l'importance de la β -diversité multi-trophique sur le fonctionnement des écosystèmes est de l'ordre de celle des changements des propriétés édaphiques. En particulier, dans cette première étude, le changement de composition de la communauté de plantes et du sol dans son ensemble était un prédicteur direct important de la multifonctionnalité (β -diversité multi-trophique totale). Cela n'était pas dû aux variations indépendantes de richesses entre les groupes trophiques (β -diversité verticale). En revanche, cela semblait être lié à l'effet direct des changements de composition au sein de certains groupes clefs (β -diversité horizontale des groupes de champignons saprophytes), couplé à l'effet indirect, via les interactions entre les groupes, des changements de composition des autres groupes trophiques. Ce résultat souligne d'une part l'importance des champignons saprophytes et de leur activité de décomposition pour le fonctionnement des écosystèmes alpins, et d'autre part l'importance des interactions entre groupes trophiques pour prédire la multifonctionnalité des écosystèmes. Il soulève ainsi de nouvelles questions : *Existe-t-il, à large échelle, une régulation trophique des décomposeurs et de leur activité de décomposition ? Comment mieux prendre en compte les interactions trophiques entre les groupes trophiques ?* Dans ce deuxième chapitre, nous nous concentrons sur l'activité de décomposition microbienne. Pour ce faire, nous tentons de mieux définir les groupes trophiques et de mieux prendre en compte les interactions qui lient les microbes et leurs

consommateurs. Ainsi, nous faisons un pas de plus vers l'intégration des réseaux trophiques dans les études du lien entre environnement, communauté du sol et leur fonctionnement.

Ce deuxième chapitre est présenté en anglais, et il est formaté et quasiment prêt pour être soumis à Ecology Letters.

Finally, in the first chapter, we studied the effects of the environment and soil communities on different ecosystem functions separately, and on the multifunctionality of the ecosystem. We showed that the links between environment, different trophic groups, and ecosystem functioning depend on the ecosystem functions studied. In a surprising way, in our first study, the change in plant composition was not directly linked to changes in productivity, whereas the change in composition of saprophytic fungi was a good predictor. This result highlights the importance of decomposition for plant communities. It challenges the hierarchical view of environment – plant community and soil – multiple ecosystem functions used in this chapter, and poses new questions: *Quels aspects de la communauté microbienne permettent de prédire correctement la structure et la productivité des communautés de plantes ? Comment la communauté microbienne (caractérisée par ses traits et sa fonction de décomposition) et la communauté de plantes (caractérisée par ses traits et sa productivité) s'associent-elles spatialement le long de plusieurs gradients d'altitude ?*

We will focus on these questions in a third and a fourth chapter.

Chapitre 2, Differential effects of soil food webs on decomposition in mountain ecosystems



Decaying tree trunk

Camille Martinez-Almoyna¹, Amélie Saillard¹, Lucie Zinger², Clément Lionnet¹, Arnaud Foulquier¹, Ludovic Gielly¹, Gabin Piton¹, The Orchamp Consortium, Tamara Münkemüller¹ & Wilfried Thuiller¹

¹ Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, 38000 Grenoble, France

² Institut de Biologie de l'ENS (IBENS), Département de biologie, École normale supérieure, CNRS, INSERM, Université PSL, 75005 Paris, France

Keywords: trophic regulation, ecosystem functioning, multitrophic communities, structural equation modelling, mountain ecosystems.

ABSTRACT

Soil food webs are pivotal actors of biogeochemical cycles, particularly decomposition. However, few studies have yet related the composition of bacteria, fungi and their respective consumers to decomposition activity, conditionally to environmental variations. Here, along multiple elevational gradients in the French Alps, we measured how the composition of fungal and bacterial communities, and their respective consumers, drove decomposition activity and whether these effects differed between forests and grasslands.

We found that while environmental effects varied little between the two habitats, decomposition activity was driven by fungal composition in forests and bacterial composition in grasslands. Importantly, we measured an indirect effect of the consumer groups, highlighting the importance of a trophic regulation that varied between habitats.

The hierarchical integration of the environment and the soil food web to quantify indirect and direct pathways effects on decomposition highlights the need to better assess the importance of trophic regulation to predict ecosystem functioning.

INTRODUCTION

Soil biodiversity underpins a range of crucial ecosystem functions and services for human well-being, including litter decomposition, carbon storage and water quality. Understanding and predicting the consequences of environmental changes for soil biodiversity and associated ecosystem functions is therefore a key challenge (Wall *et al.* 2010; Jansson & Hofmockel 2020). Addressing this challenge has generated a recent surge in global soil biodiversity syntheses, with efforts towards documenting global-scale diversity patterns of single taxa such as bacteria (Delgado-Baquerizo *et al.* 2018), fungi (Tedersoo *et al.* 2014), nematodes (van den Hoogen *et al.* 2019) or protists (Oliverio *et al.* 2020) and identifying their environmental drivers. However, we still poorly understand how community composition of these taxa drive specific ecosystem functions such as decomposition. Soil organisms from different taxa do not act independently from each other. Bacteria and fungi interact in their important role as decomposers of organic matter but also compete with each other and serve as food for nematodes and protists in the soil food web (Thakur & Geisen 2019). To better understand soil diversity effects on decomposition we need to better understand the regulating effects of soil food webs, and how this regulation changes along environmental gradients and habitats. This is a critical gap of knowledge towards predictive soil ecology.

Soils teem with an immense diversity of animals and microbes playing various roles in the decomposition of dead organic matter (e.g. plant litter) and interacting in different ways with each other (e.g. trophic or competitive interactions, Wardle *et al.* 2004). In addition, the activity of all these organisms is context dependent and varies with soil, vegetation and climatic conditions. Soils are intrinsically heterogenous and various quantities and qualities of litter with different decomposability and at different decomposition stages are mixed (Baldrian 2014). Litter strongly varies with the type of habitat and associated vegetation. For example, in temperate forests, lower litter quality with high organic matter content and more acidic soils promotes the dominance of oligotroph microbiota including many fungi species but also some bacterial clades (López-Mondéjar *et al.* 2020). Oligotrophs invest in a conservative life strategy with slow growth, but a high capacity to use complex forms of carbon immobilized in recalcitrant litter (Fontaine *et al.* 2003; Fierer *et al.* 2007). Reversely, open-habitats (e.g. grasslands), with high nutrient availability and low organic matter content foster the dominance of copiotroph microbiota including many bacterial species but also some fungal groups (Ruess & Ferris 2004). Copiotrophs invest in fast growth, but rely preferably on labile carbon and nutrients (Fierer *et al.* 2007; Ho *et al.* 2017). Past work linking gradients of litter quality and quantity to microbial strategies has focused on the role of fungi vs. bacteria ratios ignoring the more complex distribution and interactions of fungal and bacterial taxa along the economic spectrum from oligotroph to copiotroph taxa (e.g. de Vries *et al.* 2012).

Recent work underlines that the decomposition of organic matter can be described by the microbial decomposition activity (e.g. measured via extracellular enzymatic activity, Sinsabaugh *et al.* 2009; Burns *et al.* 2013) which itself depends on the soil microbial community composition and investment strategies (Piton *et al.* 2020a). A high investment in extracellular enzymes indicates a dominance of oligotroph strategies, while a low investment is linked to a dominance of copiotroph strategies (Fontaine *et al.* 2003; Piton *et al.* 2020b). However, the

effect of trophic regulation on microbial community structure and thus indirectly on its decomposition activity remains largely unexplored (Thakur & Geisen 2019). Consumers can indeed affect the composition of the microbiome, for example by preferential feeding (reported for bacteria- and fungal feeding nematodes, collembola, mites, Ruess *et al.* 2000; Schneider & Maraun 2005; A'Bear *et al.* 2014), which results in consumer release for the non-preferred taxa, and thus indirectly influence decomposition (Crowther *et al.* 2012; Trap *et al.* 2016; Thakur & Geisen 2019). Some authors suggested that this indirect regulation by microbial consumers can exceed their direct effect on ecosystem functions (Hättenschwiler *et al.* 2005). However, so far, we know little about how this regulating role of the soil food web affects decomposition at biogeographical scales and even less about its context dependency.

In mountain ecosystems, climate warming of soils leads to increased respiration and nutrient availability and thus to more copiotroph soil decomposition strategies (Donhauser & Frey 2018; Winkler *et al.* 2018; Hagedorn *et al.* 2019; Looby & Martin 2020). But we ignore the regulatory role of microbes and their feeders in this expected shift. To answer this question, we analyze how trophic regulation by microbial-feeding organisms and microbial diversity influence decomposition along elevational gradients in two contrasted habitats, forests and open habitats. We use extra-cellular enzymes to estimate microbial decomposition activity and environmental DNA extracted from the same soil cores to describe local multi-trophic communities of fungi, bacteria and their respective consumers. We then built structural equation models to address the following questions:

What are main drivers of decomposition activity and are they habitat dependent?

What is the role of microbiome diversity and foodweb control on decomposition?

Does the relative importance of bacteria vs. fungi channels depend on habitat?

MATERIEL & METHODS

Study sites: alpine elevational gradients characterized by two habitats

We studied the composition of soil communities along 18 elevational gradients of the long-term observatory ORCHAMP (<www.orchamp.osug.fr>, see Appendix S1 in Supporting information) in the French Alps. The gradients were selected to: 1) be continuous from about 900m to 3000m, 2) have homogeneous exposure and slope, 3) to best represent the environmental and topographical variability of the French Alps. Between 2016 and 2018, a minimum of five sampling plots (30*30m, see Figure A1, Appendix S1 for details) were placed along each elevation gradient, with an average of 200m elevation difference, resulting in a total of 37 forest sites and 64 open-habitat (i.e. grasslands) sites (see Figure A2, Appendix S1 for details).

Climatic data

In mountain ecosystems, the presence of snow determines 1) the starting point and 2) the length of the growing season and 3) the exposure of the soil to freeze-thaw cycles, which are key drivers of the composition and dynamics of the microbiome (Edwards *et al.* 2007; Zinger *et al.* 2009). To best characterize the average length and intensity of the growing season, we calculated growing degree days (GDD) and the intensity of freezing events (freezing degree days, FDD) in each plot. These variables were calculated as the annual sums of average daily degrees above (GDD) and below zero (FDD), modelled within the first soil horizon (10 cm depth) and averaged over 1988–2018 (see Martinez-Almoyna *et al.* (2020), table 1, for more details). GDD and FDD were calculated from the SAFRAN- SURFEX/ISBA-Crocus-MEPRA reanalysis (Durand *et al.* 2009), a model which addresses meteorological and snow conditions in mountainous regions based on large-scale topographical features.

Soil sampling, physico-chemical properties and total exoenzymatic activity

In each plot with homogeneous vegetation, we sampled soil in three 2x2m subplots that were located between 2 and 12 m apart from each other (Figure A1, Appendix S1), paying particular attention to avoid any human- and sample cross-contamination. In each subplot, we collected ten cores of superficial soil (10 first cm depth x 5 cm diameter) and ten soil cores of profound soil (second layer of 10 cm depth x 5cm diameter) to correctly describe the first soil horizon of all plots. The cores of superficial soil were pooled and homogenized separately from the more profound ones, resulting in two composite soil samples by soil subplot. In total, we thus collected 606 soil samples over the three years, among which 222 in forests and 384 in open-habitats.

We immediately retrieved 15g per soil samples for subsequent environmental DNA (eDNA extractions), and sieved the remaining parts with 5.6mm-sieves. We then froze 2.75g of the sieved sample for subsequent exoenzyme analyses, 5g to quantify water content, and kept the rest for physico-chemical analyses (soil pH, soil organic matter (SOM) and soil C/N as described in Martinez-Almoyna *et al.* (2020).

We estimated exoenzymatic activity of seven exoenzymes involved in the decomposition of C-rich substrates (EEC: α -Glucosidase (AG), β -1,4-Glucosidase (BG), β -D-Cellobiosidase (CB) and β -Xylosidase (XYL)), N-rich substrates (EEN: β -1,4-N-acetylglucosaminidase (NAG) and leucine aminopeptidase) and P-rich substrates (phosphatase (PHOS)) using standardized fluorimetric techniques (Bell *et al.* 2013, see also Martinez-Almoyna *et al.* (2020) for more experimental details). We calculated the total potential extracellular enzymatic activity (total EEA) as the sum of the potential enzymatic activities of the seven exoenzymes. We divided total EEA by SOM because SOM and microbial biomass are tightly linked, and we here study soil biodiversity effects (and not microbial biomass effects). For the sake of simplicity, we call this standardized variable decomposition activity in the rest of the MS.

Soil eDNA extraction, amplification, sequencing and curation

From the 15g per soil samples, we conducted the soil eDNA extraction immediately in the field. For eDNA amplification, we targeted Eukaryotes, Fungi and Bacteria using respectively the DNA markers Euka02 (18S rRNA), Fung02 (ITS) and Bact01 (16S rRNA) described in Ohlman *et al.* (2018). We added unique eight-base long tags at the 5' end of each primer so that the sample of origin of each sequencing read can be retrieved after sequencing. Four PCR-replicates were amplified by PCR for each sample and control. Finally, we pooled purified products together before sequencing. Sequencing was performed by pair-end sequencing on Illumina HiSeq 2000 platform (2*125 for Euka02, and 2*250 for both Bact01 and Fung02) at Fasteris, Geneva, Switzerland. Data were divided into 4 libraries for sequencing (2016, 2017 A&B, 2018, see Appendix S2-1 for more experimental details).

We curated the sequencing reads using the obitools package (Boyer *et al.* 2016) and the R package metabar (Zinger *et al.* 2021, Figure S2-A1). We first assembled paired-end reads, retrieved their original samples and marker, dereplicated them with OBITools. We also tagged and removed the PCR-errors, and clustered sequences in molecular operational taxonomic units (MOTUs). Cross-samples, reagent, sequencing contaminants and dysfunctional PCRs were removed using metabar according to conservative quality check criteria. After this step, we removed samples with only two or less remaining PCR-replicates. 562 samples remained after curation, among which 212 of forests and 350 of open-habitat soils. Then we assigned MOTUs to a taxonomical path using different databases depending on the marker and we removed low-quality MOTUs. We aggregated libraries after assignment to a trophic class and trophic group (see below), and did a second clustering step to uniformise MOTUs over the four libraries. For more details see Figures S2-A1, A2 & Tables S2-A1, A2.

Trophic groups and MOTUs functions

Focusing on decomposition, we retained only the organisms directly involved in decomposition activities (i.e. fungi and bacteria) and the organisms feeding upon fungi and bacteria to measure the importance of their trophic regulation. Instead of analyzing every single organism, we calculated meaningful measures of diversity and composition designed at two levels of aggregation: *trophic class* (e.g. fungi) and *trophic group* (e.g. saprophytic fungi). Each

MOTU was then assigned to a trophic class and a trophic group based on its function in the ecosystem and its preys and predators (Elton 1927; Gauzens *et al.* 2015, Figure S2-A2).

Trophic class level: Both fungi and bacteria MOTUs retrieved from their respective markers were assigned to the fungi and bacteria trophic classes. We kept them separated because exoenzymes production is a common function among these taxa, but their metabolic functions do not fully overlap and they are often in competition (De Boer *et al.* 2005; Purahong *et al.* 2016). We refer to the trophic classes of bacteria and fungi together as the microbiome. Protists were considered in the trophic class of microbial consumers, as in Thakur & Geisen (2019).

We then classified consumers in two other trophic classes (bacteria- and fungi consumers) from the euka02 marker using literature, expert knowledge and databases (Figure S2-A2). Among taxa eating bacteria, we mostly found protists and nematodes in our samples, and for fungi, we mostly found acari and springtails. We removed the MOTUs referenced as feeding on both bacteria and fungi as they were very rare (only 15 MOTUs in the data set). We are aware that this classification may, in some cases, only represent the preferred (and not an obligatory) diet (Geisen 2016), but these groups and consumer-prey linkages represent the extent of knowledge we were able to extract from literature and current databases. Details on the number of MOTUs of each trophic class are in Appendix 2, Table S2 – A3.

Trophic group level: We further associated MOTUs within each trophic class to more resolved trophic groups, to help with the interpretation of the compositional variation within the trophic classes. We respectively assigned the MOTUs belonging to the trophic classes of fungi and bacteria to trophic groups using FUNGuild and FAPROTAX (Louca *et al.* 2016; Nguyen *et al.* 2016). We then simplified the FAPROTAX functions using expert knowledge and literature (Figure S2-A2). Within the trophic classes of bacteria-consumers and fungi-consumers, we used the taxonomy to further associate the MOTUs to trophic groups, since close-related taxa overwhelmingly show close functions (Wiens *et al.* 2010; Potapov *et al.* 2016; Schaefer & Caruso 2019). We provide details on the number of MOTUs within each trophic group in Appendix 2, Table S2 – A3.

Statistical analyses

To answer our set of questions, we needed to analyse how the composition of the food-web (fungi and bacteria, and consumers of fungi and bacteria) and thus the composition of each of these classes influence decomposition, while accounting for the effects of the environment. First and independently for each of the two habitats and each of the four trophic classes, we used a correspondence analysis to structure the samples based on their MOTUs compositions along a single major “composition” axis. Second, we used structural equation modelling for both forests and open-habitats independently to quantify how decomposition was driven directly by the composition of fungi and bacteria and how it was indirectly regulated by the composition of primary consumers.

Compositional change between samples

To quantify how different samples vary in composition for the four trophic classes (bacteria, fungi, bacteria-consumers, fungi-consumers), we carried out a correspondence analysis (CA) for each trophic class (MOTUs-sample matrix) for both forests and open-habitats (i.e., eight CAs in total). We then extracted the position of each sample on the first axes of the CAs and use this as a measure of composition of the trophic classes in the following. Two samples with similar positions have thus similar compositions.

Then, to better visualize and understand what structured the position of the samples on the CA axes, we used the trophic group information of each MOTU to model their relative abundance per sample as a function of their positions on the CA axes. For each trophic group of each trophic class and for both forests and open-habitats, we then fitted a general linear model with the relative abundance of each trophic group per sample as a response variable and the sample position on the respective CA axis as an independent variable (Appendix S3, Figures S3-A1, A2).

Structural Equation Modelling

For each habitat (forests and open-habitats), we built a structural equation model (SEM) to quantify how the environment (climate and soil) directly affect the composition of each trophic class and decomposition, whether and how the composition of fungi and/or bacteria drive decomposition, and whether and how the composition of primary consumers further affects the compositions of fungi and bacteria (and thus indirectly decomposition).

We first tested a priori model structure using the `sem` function (R-package `piecewise`, Lefcheck 2016). This function estimates the path coefficients locally and then assesses the fit between the a priori model and the data by testing the conditional independence of variables that are not linked by a path (Shipley 2000). Second, when necessary, we added some of the missing paths based on their ecological relevance for our models (Grace *et al.* 2010). Finally, we optimized the model structures by a stepwise removal of the non-significant relationships, and while evaluating the effect of each removal on model quality assessed with BIC (de Vries & Bardgett 2016; Hertzog 2018; Piton *et al.* 2020a). For interpretations, we used the standardized coefficients extracted from the most parsimonious models (Grace *et al.* 2010).

RESULTS

The effects of climate, soil and biotic factors on decomposition activity vary between habitats

The two structural equation models for forests and open-habitats allow explaining a very similar and important percentage of total variation ($R^2=16\%$) in decomposition across the multiple soil samples. Interestingly, while they are close in term of explained variance, the strengths of the paths strongly differ between forests and open-habitats (Fig. 1 & 2). In forests, decomposition activity was strongly influenced by growing and freezing degree days, to a lesser extent by soil C-N ratio and least but still significantly by the composition of the fungi class (Fig. 1). In contrast, for open-habitats, the composition of the bacteria class was the primary factor while climate and soil play a similar and moderate role in explaining decomposition activity (Fig. 2). Interestingly, in both habitat types, there was a negative relationship between GDD as well as FDD and decomposition activity. In other words, the less optimal were the conditions in terms of energy intake in the growing season (i.e. low GDD) and the least metabolic activities were physiologically slowed down by freezing temperatures (i.e. low FDD), the stronger the overall microbial investment in enzymatic activities to decompose litter.

Microbiome diversity and foodweb regulation mediate environmental effects on decomposition activity

To clarify the overall indirect influence of the environment through either the microbiome directly or through an additional foodweb regulation, we extracted from the structural equation models the indirect standardized effects of the environment through the consumers and the microbiome (Fig. 3). Overall, there was a drastic difference between forests and open-habitats, with an overall lower effect of environment through the indirect pathways in forests compared to open-habitats (Fig. 3).

In forests, soil pH drove the composition of bacteria-consumers, with communities dominated by the trophic group Rhizaria preferring acidic soils, and communities with a co-dominance of Rhizaria and Ciliophora groups preferring higher pH (Fig. 1 (A), Fig. S3-A1-A). Bacteria consumers strongly affected the composition of bacteria, with Rhizaria dominated consumer communities leading to a dominance of saprophytic bacteria, especially on acidic soils (Fig. 1 (A, C), Fig. S3-A1-A, C). Under more moderate pH and more diverse consumer communities, the bacteria communities became more diverse as well. The composition of fungi consumers was primarily driven by soil organic matter quality with low soil organic matter quality (i.e. high C/N) leading to communities dominated by acari and a co-dominance between acari and springtail groups with higher soil fertility (Fig. 1 (B), Fig. S3-A1-B). Fungi-consumers were not directly linked to fungi but the composition of bacteria-consumers moderately affected fungal composition. In addition, higher pH, higher thermal energy intake (i.e. GDD) and higher soil organic matter quality (i.e. lower C/N) fostered mycorrhiza dominance in fungal composition which in turn reduced decomposition activity (Fig. 1).

In open-habitats, the biotic control on decomposition was radically different than in forests. On the one hand it was much stronger overall and on the other hand both microbiome composition

and foodweb regulations played important roles (Fig. 2, 3). The compositions of bacteria-consumers and bacteria were mostly driven by soil pH and bacteria consumers had a strong influence on bacteria. Compositional trends and biotic links followed exactly the same trends in trophic group dominance as in forests (Fig. 2 (A), Fig. S3-A2-A). Bacteria composition affected decomposition strongly with high saprophytic bacteria dominance leading to high decomposition activities. The composition of the fungal class was strongly driven by soil pH, affected by bacteria composition but not significantly influenced by the fungi-consumers and did not affect decomposition activity.

In sum, the effects of microbiome diversity and foodweb regulation on decomposition activity was highly habitat dependent. In forests, the weak overall effect on decomposition was mainly driven by microbiome community composition, while in open-habitats both microbiome composition and foodweb regulation strongly affected decomposition activity.

Teasing apart the role of biotic channels in decomposition activity

To clarify the overall influence of either the fungi or the bacteria channels, we extracted from the structural equation models the indirect standardized effects through the respective consumers and microbiomes (i.e. channels, Fig. 4). We found a full switch between biotic channels when comparing forests and open-habitats. In forests, the fungi channel drove the overall moderate and microbiome-based biotic effect on decomposition activity. In open-habitats, the bacteria channel strongly drove environmental indirect effects on decomposition via soil biodiversity but also via strong foodweb regulation (Fig. 4).

DISCUSSION

While the overwhelming role of the soil microbiome in soil ecosystem functioning is increasingly recognized, the respective effects of environment, soil diversity and foodweb regulation on decomposition activity at biogeographical scales were poorly understood so far (Thakur & Geisen 2019). Here, we assess the role of four important environmental variables and the main consumers of the microbiome in shaping the composition and activity of the microbiome, in two different habitats and along several environmental gradients in the French Alps. Using structural equation models, we found that (i) climate and soil physico-chemical properties affect both soil biodiversity involved in the decomposition process and the decomposition process itself, (ii) decomposition activity was regulated by the microbiome and its consumers but this regulation was context dependent, and (iii) in forests soil diversity effects were moderate and dominated by fungi while in open habitats effects on decomposition were much stronger and driven by bacteria with bacteria consumers strongly regulating these processes.

Direct effects of environmental variables on decomposition activity were strong and comparable in forests and open-habitats. Climate was a primary direct determinant of decomposition activity and was much more influential than soil physico-chemical properties. An interesting result was the negative relationships between both GDD and FDD and decomposition activity. These results nicely fit to the hypothesis that a strong investment in decomposing litter can be driven either by physiological limits or, if conditions are above physiological limitation, by a switch in energy economic strategies (Piton *et al.* 2020b). Interestingly these two drivers lead to results that may look contradicting at first glance: High FDD indicates frequent and strong freezing that physiologically limits all metabolic processes and thus also production of enzymes (Sorensen *et al.* 2018). On the other hand, high GDD indicates high energy input and -through feedbacks with vegetation- higher quality litter and soil fertility, thus fostering copiotroph strategies with lower strategic investment in decomposition activity (Fontaine *et al.* 2003; Piton *et al.* 2020b).

In this study, we also bring new insights in the environmental drivers of the composition of the soil multi-trophic assemblages by showing that soil physico-chemical variables are crucial determinants of four important trophic classes of the soil food-web. These observed effects are more pronounced than those from relevant climatic variables. In particular, the importance of soil pH was a particular structuring force of bacteria, bacteria-consumers and fungi community composition (Fig. 1 & 2). The importance of pH for bacteria diversity and composition has been demonstrated at global and regional scales (Fierer & Jackson 2006; Griffiths *et al.* 2011; Donhauser & Frey 2018; Looby & Martin 2020). Fierer *et al.* (2006) suggested that bacteria have quite narrow pH ranges for optimal growth and that non-neutral soil pH imposes an important stress to bacteria. Indeed, their internal pH needs to be maintained close to neutral, and therefore pH acts as a strong environmental filter for specific bacterial trophic groups. In agreement with this hypothesis, we demonstrated an increase of the diversity of bacteria communities towards more neutral pH, while relatively acidic pH resulted in the dominance of saprophytic groups (Fig. 1 (C) & Fig. 2 (C)). The effects of pH on fungal composition is more controversial with some papers showing no response of fungi to pH (Rousk *et al.* 2010a), and

others showing the opposite (Tedersoo *et al.* 2014). In our case study, the response of fungal communities to pH followed the opposite trend than for bacteria, with higher trophic diversity in more acidic soils than in neutral soils. However, this may be also driven by competition with bacteria as supported by their negative biotic links in our structural equation models (Fig. 1 and Fig. 2). More surprising was the strong relationship between bacteria-consumers, mostly protists, and soil pH. Indeed, a global study of protists' biogeography found that the community composition of protists was shaped mostly by climatic factors (Bates *et al.* 2013), and a more local study confirmed that protist distributions in mountain environments were better predicted by topographic predictors than edaphic ones (Seppey *et al.* 2020). However, most bacterivorous protists in our study belong to the Ciliophora and Rhizaria clades that have recently been shown to be strongly affected by soil pH (Oliverio *et al.* 2020). More generally, the determinants of composition of bacterivores and even fungivores have been poorly studied so far (Geisen *et al.* 2019; Thakur & Geisen 2019; Chu *et al.* 2020; Fiore-Donno *et al.* 2020). Further research is needed to understand the environmental drivers of soil foodweb composition, since soil diversity can directly and indirectly influence ecosystem functioning.

In respect to our second question, we demonstrated the importance of a top-down regulation in the soil food web on decomposition activity. Most of the indirect effects of the environment on decomposition activity were due to a foodweb regulation, i.e. via top-down associations between the microbiome compositions and its consumers. In particular, the link between the composition of bacterivores and bacteria was pivotal in our two habitats (Fig. 1, Fig. 2). This result corroborates the high degree of specificity that was already observed for bacterivore grazing (Adl & Gupta 2006; Trap *et al.* 2016). For example, this is notorious that bacterivorous protists and bacteria have coevolved thanks to their trophic interactions, and that the presence of specific groups of protists and nematodes influence the overall composition of the microbiome (Griffiths *et al.* 1999; Geisen *et al.* 2018; Gao *et al.* 2019). This might explain why the composition of bacterivores seemed to negatively affect the fungal composition in forest habitats, some protist groups being quite generalist in their feeding behaviors (Geisen 2016). In contrast, the effect of fungal grazers on the composition of the microbiome and on its function are much more contrasted in the literature (Hanlon & Anderson 1979; Maraun *et al.* 2003; Crowther *et al.* 2012). Fungi grazers are likely less specific, and their compositional turnover does not seem to affect fungal communities' composition (Crowther *et al.* 2012). Moreover, due to the length of the mycelia, their grazing effect is less drastic. Up to a certain grazing pressure, they do not suppress the whole individual and can even enhance fungal growth and activity (Hanlon & Anderson 1979; Crowther *et al.* 2012). Taken together, this likely explains the weak links we found between the compositions of the fungi-consumers and the microbiome (Fig. 1, 2, 4).

Finally, we found that the relationship between soil food webs and decomposition activity clearly depended on the habitat type. Decomposition activity was directly determined by the composition of fungi in forests, while the composition of bacteria played a major role in open-habitats. This confirms the work of Schneider (2010, 2012) who showed that most of the exoenzymes found in forest soils are from fungal origin. Indeed, some trophic groups of fungi have already been shown to be key drivers of particularly recalcitrant organic compounds of forest litter (e.g. lignin, tannins). For example, the 'white-rot' fungi are saprophytic fungi whose

activity is necessary to degrade lignin (De Boer *et al.* 2005). By breaking down lignin, such saprophytic fungi allow other microorganisms to access other organic compounds (e.g. cellulose) protected in forest plant debris, which could explain the association between an overall higher investment in decomposition activity and a higher relative abundance of saprophytic fungi in our study (Fig. 1, De Boer *et al.* 2005). Open-habitats are instead characterized by plants easier to decompose, because they typically contain fewer resistant compounds like lignin. Thus, the release of the aforementioned constraints could explain the strong link between the composition of bacteria and decomposition activity in open-habitats (Fig. 2). Compared to forests, open-habitats also contain less organic matter and greater amounts of mineral nutrients in general, which also favors copiotroph strategies (Fierer *et al.* 2007). Moreover, autotrophy has been shown to be enhanced in cold open-habitats with high availability of labile nutrients (Guo *et al.* 2015). This may underlie the association between reduced investment in decomposition activity and increased relative abundance of autotroph bacteria groups in our study. Finally, a change of the competitive success of bacteria and fungi could participate to the differences we observed between forests and open-habitats. Indeed, we found that fungi and bacteria compositions were more strongly linked in open-habitats than in forests, possibly mirroring a stronger direct competition in open-habitats than in forests. This again could be explained by the difference in the litter quality and soil physico-chemical properties. Less acidic soils due to a less recalcitrant litter in open-habitat might release the environmental stress imposed by low pH on bacteria, making them more competitive in open-habitats (Rousk *et al.* 2010b). In sum, our results support many of the hypotheses derived from smaller scale observations and experiments at geographical scales and allow contrasting pathways in forests vs. open-habitats. It would be interesting now to go back to more experimental studies to test our explanation approaches and to help understanding the biological mechanisms underlying the patterns we observed at macro-scales.

Conclusion

There is a strong need to get a better understanding of the role of the soil food web in ecosystem functioning and how this role might be affected under current but also future environmental conditions. Here, we demonstrate how complex are the direct and indirect effects of environment on one ecosystem function, decomposition activity, and how top-down regulation through the food web can affect the outcome of decomposition. This study calls for further analysis of trophic regulation of ecosystem functioning and in particular of the multi-functionality of ecosystems. The incorporation of multi-trophic interactions into this understanding seems to open up natural avenues towards a better understanding and modelling of the soil compartment under both current and future conditions.

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Author statement

CMA, TM and WT conceptualized the overall study and methodology. WT, AS, CMA, TM and the ORCHAMP Consortium collected the soil data. LG, GP and AS carried out the lab work for eDNA extractions, PCRs and measures of exoenzymatic activities and soil properties. CL run the bioinformatic pipelines. LZ helped with the trophic assignment and bioinformatic pipelines. CMA run all statistical analyses. CMA, TM and WT led the interpretation of the results. CMA drafted the initial draft of the paper together with WT and TM. All authors contributed to editing and finalizing the paper.

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Figure captions

Figure 1 | Structural equation modelling of the effects of environment and soil food web on decomposition in forests. Arrow sizes are proportional to the associated path coefficients. Paths with double arrows represent correlations. The external panels represent the relationships between the relative proportion of each trophic group for each trophic class in function of their position along the first CA axis. We colored only the trophic groups that showed the most marked variations along the CA axis, and more detailed plots are provided in Fig. S3-A1. For example, for Bacteria-consumers, only the variations of Rh. (Rhizaria) and Ci. (Ciliophora) are represented. Other abbreviations are ii) Ac. (Acarien), Co. (Collembola), iii) Sa. B. (Saprophytic Bacteria), Zo. B. (Zooparasitic Bacteria), Ph. B. (Photoautotrophic Bacteria), iv) Sy. F. (Symbiotic Fungi), Sa. F. (Saprotrophic Fungi), a.F.F. (all Functions Fungi).

Figure 2 | Structural equation modelling of the effects of environment and soil food web on decomposition in open-habitats. Arrow sizes are proportional to the associated path coefficients. Paths with double arrows represent correlations. The external panels represent the relationships between the relative proportion of each trophic group for each trophic class in function of their position along the first CA axis. We colored only the trophic groups that showed the most marked variations along the CA axis, and more detailed plots are provided in Fig. S3-A2. For example, for Bacteria-consumers, only the variations of Rh. (Rhizaria) and Ci. (Ciliophora) are represented. Other abbreviations are ii) Ac. (Acarien), Co. (Collembola), Rh. (Rhizaria), iii) Sa. B. (Saprophytic Bacteria), Che. B. (Chemolithoautotrophic Bacteria), Zo. B. (Zooparasitic Bacteria), Ph. B. (Photoautotrophic Bacteria), iv) Sy. F. (Symbiotic Fungi), Sa. F. (Saprotrophic Fungi).

Figure 3 | Comparison of the indirect standardized effects of the environment (soil physico-chemical properties and climatic variables) via consumers and microbiome on decomposition activity, extracted from the structural equation models (Fig. 1, 2). Environmental indirect effects via consumers correspond to the sum of the effects of each indirect path, which includes the composition of a trophic group of consumers. By contrast, environmental indirect effects via microbiome correspond to the sum of the effects of each indirect path, which does not include the composition of a trophic class of consumers. The effect of each indirect path is computed as the product of the standardized path coefficients along the path.

Figure 4 | Comparison of direct and indirect standardized effects of soil food-web on decomposition activity, extracted from the structural equation models (Fig. 1 & 2). Indirect effects (hatched boxes) correspond to the sum of the effects for each indirect path, where the effect for each indirect path is computed as the product of the standardized path coefficients along the path. The sum of the direct and indirect effect is the total effect of a variable. To meet the definition of channel, we consider for this figure only the mediation via bacteria for bacteria-channel and via fungi for fungi-channel.

FORESTS

BIC = 173.202
 Fisher's C = 17.861
 P-value = 0.597

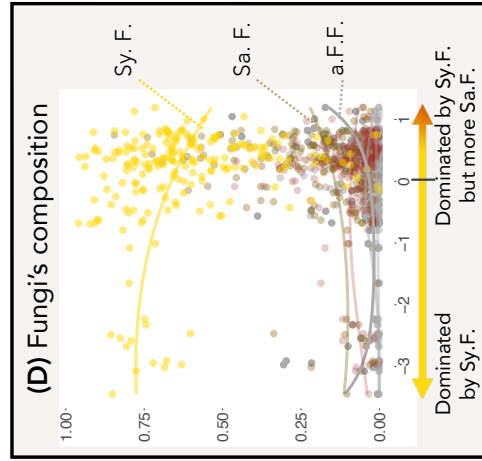
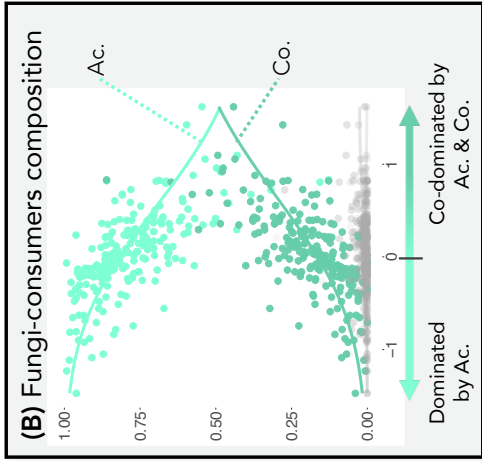
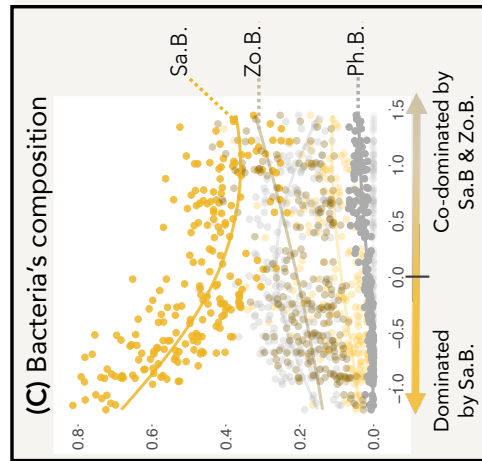
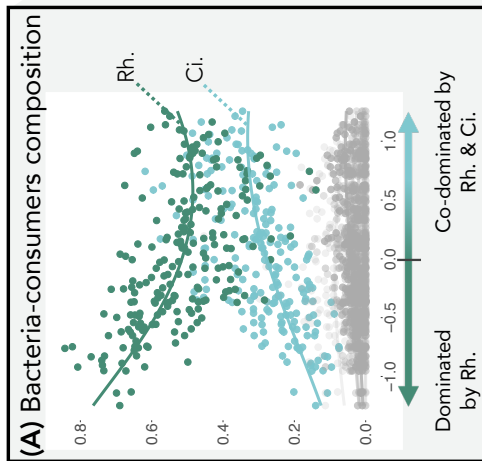
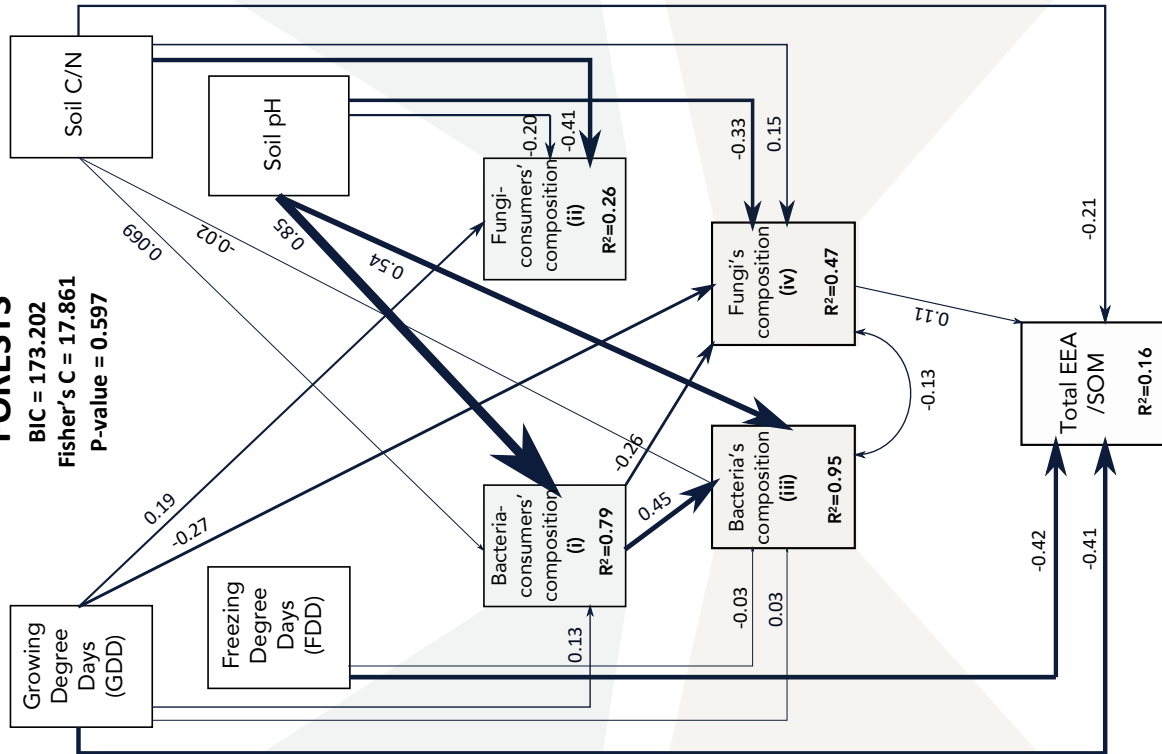


Figure 1

OPEN-HABITATS

BIC = 202.509
 Fisher's C = 20.913
 P-value = 0.182

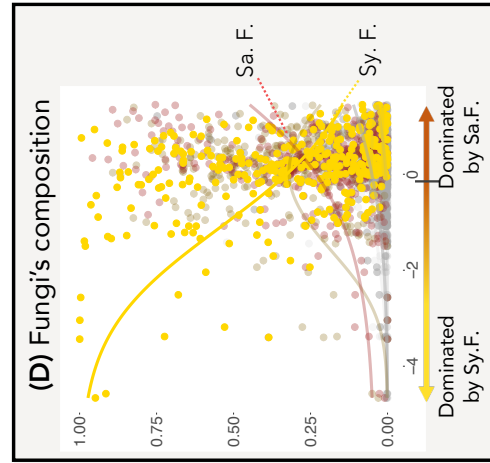
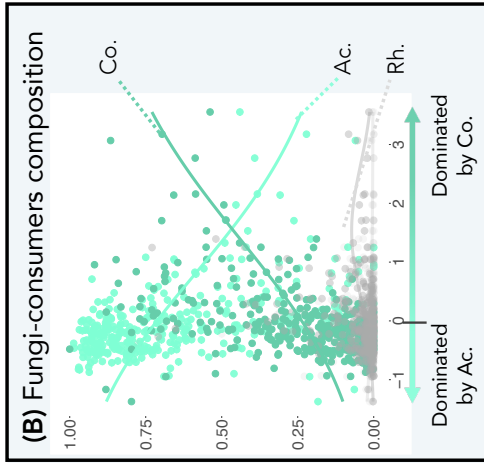
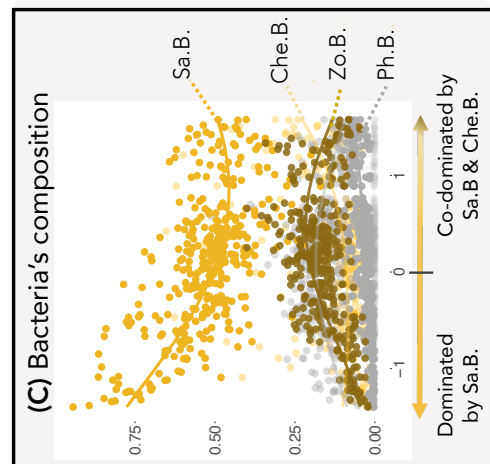
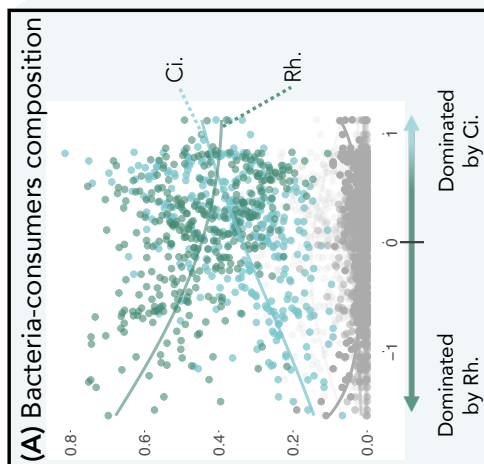
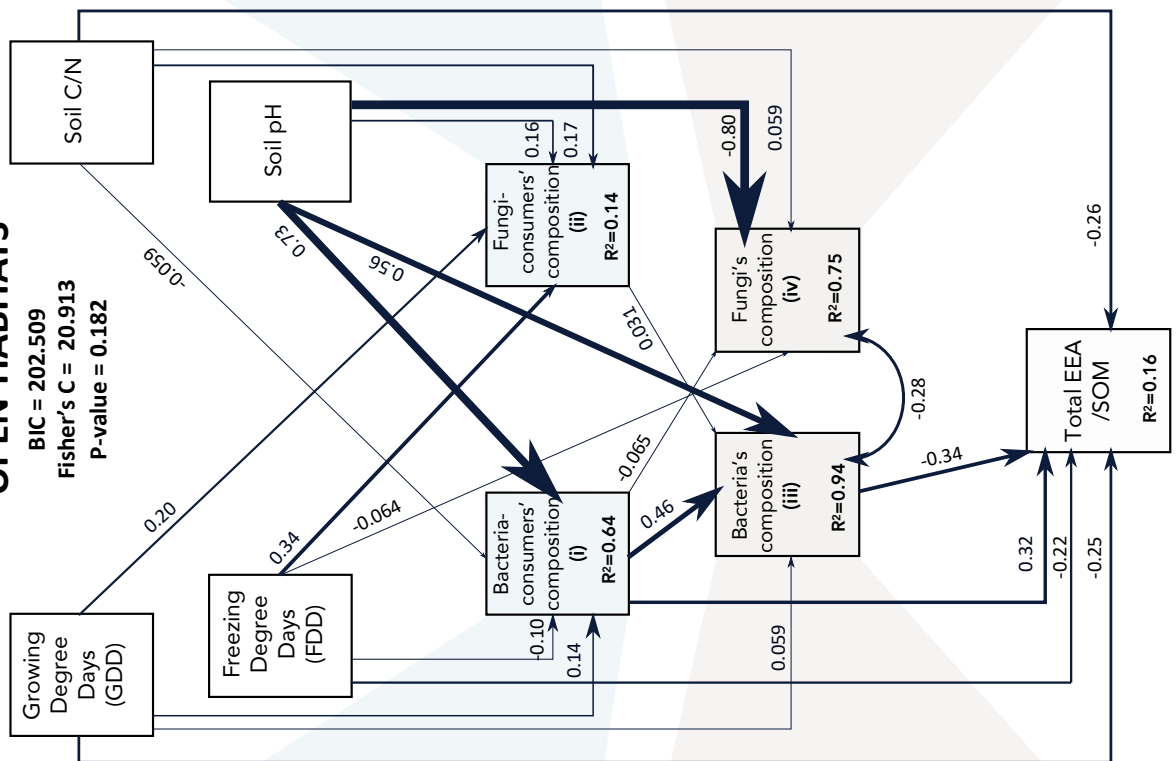


Figure 2



Figure 3

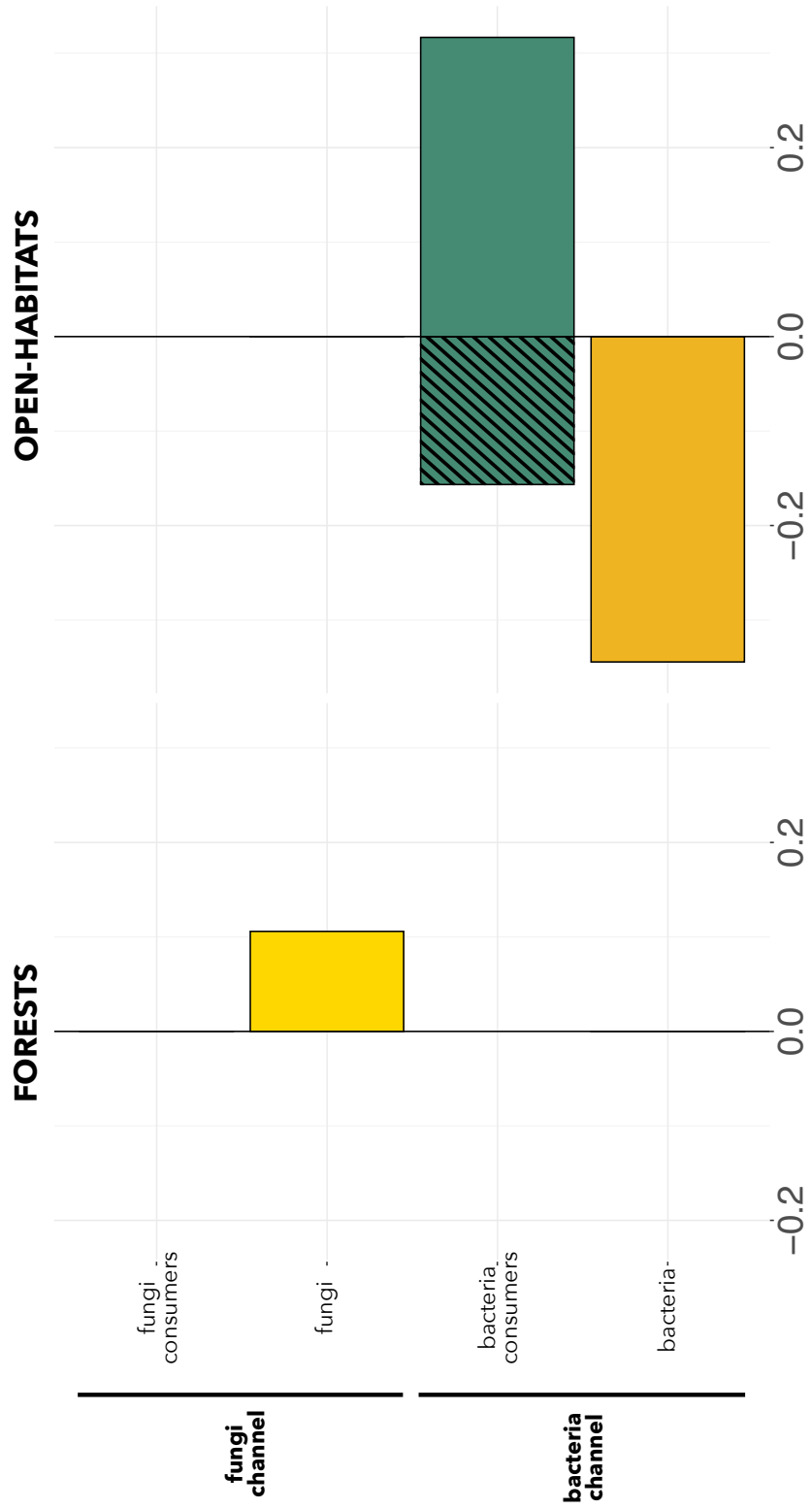


Figure 4

Du chapitre 2 au chapitre 3 ...

Dans le deuxième chapitre, nous avons fait un pas de plus vers l'intégration des réseaux trophiques dans les études du lien environnement-biodiversité-fonctionnement. En effet, nous avons intégré les interactions entre les microbes et leurs consommateurs de manière hiérarchique. Cela nous a permis de démontrer l'existence d'une régulation trophique de la décomposition microbienne, qui est particulièrement importante dans les milieux ouverts. Cette étude, qui est la première à intégrer explicitement les interactions trophiques connues entre microbes et leurs consommateurs dans une étude BEF, montre également qu'il est possible de prédire la décomposition dans l'espace géographique et à large échelle, en considérant l'environnement et les réseaux trophiques.

Cependant, cette approche hiérarchique n'est pas facile à appliquer à toutes les fonctions écosystémiques. La productivité primaire notamment, n'est pas uniquement régulée par les herbivores et leurs consommateurs, mais également par des interactions indirectes entre les plantes et la communauté du sol. Dans le premier chapitre, nous avons montré que les changements de productivité étaient particulièrement liés aux changements de composition des champignons saprophytes, alors que les changements de composition des plantes n'avaient pas d'effet significatif. Cela soulevait la question *des interrelations entre décomposeurs, décomposition, plantes et productivité primaire à l'échelle biogéographique*.

Le cadre conceptuel développé en 2013 par Lavorel *et al.*, qui propose d'utiliser des approches fonctionnelles pour prédire les effets de l'environnement et des communautés multi-trophiques sur les fonctions écosystémiques, pourrait permettre de mieux comprendre les interrelations entre décomposeurs, décomposition, plantes et productivité. Ce cadre conceptuel généralise le concept de traits de réponse et d'effet aux communautés multi-trophiques, et s'appuie sur la définition de traits **trophiques** de réponse et d'effet (INTRO, Box 2). Les traits trophiques (ou topologiques) décrivent l'interaction entre deux groupes trophiques par la réponse fonctionnelle d'un groupe trophique à l'effet fonctionnel de l'autre. Par exemple, si on applique ce cadre conceptuel aux plantes et aux microorganismes, il nécessite d'identifier des traits trophiques d'effets des microorganismes et des traits trophiques de réponse des plantes, qui décriraient l'influence indirecte des microorganismes sur la composition des communautés de plantes, via leur rôle dans le recyclage de la matière organique et la disponibilité des nutriments. En identifiant un tel lien fonctionnel entre les deux groupes trophiques, on pourrait comprendre comment les interactions multi-trophiques entre plantes et microorganismes contraignent la composition des communautés de plantes et cascaded jusqu'à leur fonction écosystémique, la productivité.

Cependant, les traits fonctionnels des microorganismes sont très peu documentés, du moins à l'échelle spécifique, ce qui interdisait jusqu'ici l'utilisation de ce cadre conceptuel, et limitait notre capacité à prédire le lien entre environnement, communautés de plantes et du sol, et fonctionnement des écosystèmes. Récemment, en revanche, il a été montré que certaines caractéristiques mesurées à l'échelle des communautés microbiennes, liées à la production d'exo-enzymes, peuvent être considérés comme des proxys des traits moyen pondérés de la

communauté microbienne. En effet, la stœchiométrie des activités exo-enzymatiques reflète l'assemblage de la communauté microbienne ainsi que sa stratégie dominante d'acquisition des ressources. La stœchiométrie des activités exo-enzymatiques impliquées dans l'acquisition du carbone, de l'azote et du phosphore est, d'une part, liée à l'optimisation de la production d'exo-enzymes pour cibler l'élément le plus limitant. D'autre part, elle pourrait refléter un compromis entre l'allocation des ressources pour la croissance (augmentation de l'investissement relatif dans les exo-enzymes pour le carbone) ou pour la production d'enzymes extracellulaires de manière générale (augmentation de l'investissement relatif dans les exo-enzymes pour l'azote et le phosphore).

Dans le prochain chapitre, nous changeons de perspective, et nous nous intéressons aux relations entre décomposeurs, décomposition et composition des communautés de plantes. Nous cherchons à identifier quels aspects des communautés microbiennes prédisent le mieux les distributions des plantes, lorsqu'ils sont mis en interaction avec des traits (de réponse) des plantes, particulièrement ceux liés à l'acquisition des ressources. Notamment, nous nous intéressons à l'effet des i/ traits fonctionnels (d'effet) microbiens, liés à leur stratégie d'acquisition des ressources, et mesurés à l'échelle de la communauté microbienne via les ratios d'activités exo-enzymatiques, ou ii/ la fonction de décomposition microbienne, mesurée à l'échelle de l'écosystème via la mesure de l'activité exo-enzymatique totale (toutes voies confondues).

Ce chapitre est présenté en anglais, et a fait l'objet d'une publication dans *Ecography* en 2020.

Chapitre 3,
Climate, soil resources and microbial
activity shape the distributions of
mountain plants based on their functional
traits.



Alpine grassland close to the elevational gradient of the Lautaret (LAU).

ECOGRAPHY

Research

Climate, soil resources and microbial activity shape the distributions of mountain plants based on their functional traits

Camille Martinez-Almoyna, Gabin Piton, Sylvain Abdulhak, Louise Boulangeat, Philippe Choler, Thierry Delahaye, Cédric Dentant, Arnaud Foulquier, Jérôme Poulénard, Virgile Noble, Julien Renaud, Maxime Rome, Amélie Saillard, The ORCHAMP Consortium, Wilfried Thuiller and Tamara Münkemüller

C. Martinez-Almoyna (<https://orcid.org/0000-0002-3624-7932>) ✉ (cmartinezalm@gmail.com), G. Piton, L. Boulangeat, P. Choler, A. Foulquier, J. Renaud, A. Saillard, W. Thuiller (<https://orcid.org/0000-0002-5388-5274>) and T. Münkemüller, Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Grenoble, France. – S. Abdulhak, Conservatoire Botanique National Alpin, Domaine de Charance, Gap, France. – T. Delahaye, Parc National de la Vanoise, Chambéry, France. – C. Dentant, Parc National des Ecrins, Domaine de Charance, Gap, France. – J. Poulénard, Univ. Savoie Mont Blanc, Univ. Grenoble Alpes, CNRS, EDYTEM, Chambéry, France. – V. Noble, Conservatoire Botanique National Méditerranéen de Porquerolles, Hyères, France. – M. Rome, Univ. Grenoble Alpes, CNRS, SAJF Grenoble, France.

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While soil ecosystems undergo important modifications due to global change, the effect of soil properties on plant distributions is still poorly understood. Plant growth is not only controlled by soil physico-chemistry but also by microbial activities through the decomposition of organic matter and the recycling of nutrients essential for plants. A growing body of evidence also suggests that plant functional traits modulate species' response to environmental gradients. However, no study has yet contrasted the importance of soil physico-chemistry, microbial activities and climate on plant species distributions, while accounting for how plant functional traits can influence species-specific responses.

Using hierarchical effects in a multi-species distribution model, we investigate how four functional traits related to resource acquisition (plant height, leaf carbon to nitrogen ratio, leaf dry matter content and specific leaf area) modulate the response of 44 plant species to climatic variables, soil physico-chemical properties and microbial decomposition activity (i.e. exoenzymatic activities) in the French Alps.

Our hierarchical trait-based model allowed to predict well 41 species according to the TSS statistic. In addition to climate, the combination of soil C/N, as a measure of organic matter quality, and exoenzymatic activity, as a measure of microbial decomposition activity, strongly improved predictions of plant distributions. Plant traits played an important role. In particular, species with conservative traits performed better under limiting nutrient conditions but were outcompeted by exploitative plants in more favorable environments.

We demonstrate tight associations between microbial decomposition activity, plant functional traits associated to different resource acquisition strategies and plant distributions. This highlights the importance of plant–soil linkages for mountain plant distributions. These results are crucial for biodiversity modelling in a world where both climatic and soil systems are undergoing profound and rapid transformations.

Keywords: extracellular enzymatic activity, French Alps, hierarchical species distribution model, ORCHAMP, plant biogeography, trait-based model



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Introduction

Human-induced global change not only alters climate, but also soil properties and functioning (Rillig et al. 2019). Climate and soil jointly influence plant species distributions through their effect on plant growth, survival and reproduction (Buri et al. 2017). Moreover, there is a growing body of evidence that the interplay of plant functional traits with these environmental gradients shapes plant distributions (Pollock et al. 2012, Carboni et al. 2018). The framework of the ‘fast–slow’ plant economics spectrum predicts that the environment selects plants with specific functional traits, resulting in the spatial segregation of plants with different ecological strategies (Choler 2005, Reich 2014). Favorable environmental conditions select for functional trait values related to an exploitative strategy (i.e. rapid nutrient acquisition and fast growth, Aerts 1999, Reich 2014). Plants with exploitative traits lead to a soil organic matter that is easier to decompose, which increases nutrient availability, and in return favors exploitative plants. On the contrary, limiting environmental conditions promote a conservative strategy (i.e. slow plant growth but high nutrient retention capacity, Aerts 1999). Conservative plant traits induce low decomposability of soil organic matter, which slows down nutrient release in the soil, and thus selects plants with conservative trait values (Wardle and Bardgett 2002, Grigulis et al. 2013, Legay et al. 2016). Although it is well known that plants and soils are linked by feedback loops at local scales, the influence of plant–soil linkages on plant distributions is under-studied at large biogeographic scales.

One of the best-studied environmental drivers of plant success is climate (e.g. temperature, Grace 1987, Choler 2018). In mountain environments, plant success depends on the ability to grow and reproduce quickly within the short growing season. Moreover, climatic extremes such as freezing events or drought can damage plant tissues and thus limit survival (Grace 1987). In addition to climate, soil physico-chemical properties, such as pH, soil organic matter and soil C/N drive plant growth because they are related to nutrient availability (Lee 1998, Buri et al. 2017). However, measuring nutrient supply for plants is not straightforward at large spatial scales. Plant nutrient supply depends on the decomposition rate of soil organic matter by microbial communities. Many different microorganisms, mainly bacteria and fungi, produce extracellular enzymes (exoenzymes) to recycle the complex macromolecules constituting the debris of dead living organisms such as plants themselves. Different exoenzymes target different molecules and at the end of the decomposition chain, some of them enable the release of soluble monomers and finally nutrient mineralization (Sinsabaugh et al. 2008, Burns et al. 2013). Nutrient supply for plants should thus be related to the activities of exoenzymes catalyzing the terminal reactions of decomposition. The sum of the activities of the main exoenzymes in the top-soil (hereafter total EEA) has been suggested as a relevant indicator of the microbial decomposition activity (Burns et al. 2013) that makes nutrients available for plant uptake.

In soils, both the overall nutrient availability and the element stoichiometry (here we focus on the balance between carbon, nitrogen and phosphorus) are driven by the quantity and nutritional quality of plant litter inputs, and affect plant growth in return (Li et al. 2019). Microbes modulate the production of element-specific exoenzymes according to soil element stoichiometry (Sinsabaugh et al. 2008). Thus, the relative investment of microbial community in the acquisition of each type of nutrients can be used as a proxy of nutrient limitation (e.g. high activity of N-targeting exoenzymes, EEN, in comparison to total EEA, EEN/total EEA, reflects a low availability in environmental nitrogen relative to carbon and phosphorus). Finally, microbes compete with plants for nutrients dissolved in the soil solution. The relative demand of the microbial community for nitrogen compared to phosphorus can be assessed through ratios of exoenzymes (i.e. EEN/EEP, Piton et al. 2019). For example, a high EEN/EEP ratio means that plant competition with microbes will be stronger for nitrogen than for phosphorus, and might reduce nitrogen availability for plants. In sum, considering soil exoenzymes and their ratios promises an important way forward to include soil nutrient availability driven by reciprocal plant–soil linkages in plant distribution models. Moreover, accounting for plant functional traits related to nutrient acquisition strategies will allow accounting for the fact that conservative species respond in a different way to nutrient limitation than exploitative species.

In this paper, we aim to disentangle how climate, soil physico-chemical properties and microbial decomposition activity (the two latter are hereafter summarized as ‘soil properties’) influence the distributions of 44 plant species in the French Alps, while accounting for the modulating effects of plant traits. Our approach is based on a hierarchical multi-species distribution model and addresses the two following questions: 1) what are the relative influences of climate, soil physico-chemical properties and microbial decomposition activity (measured via ratios of exoenzymatic activities) in explaining plant distributions in mountain ecosystems? 2) Do species with different functional traits respond differently to gradients of climate and soil properties?

Material and methods

Study sites and species data

We studied the distributions of plant species along 18 elevation gradients in the French Alps. The gradients belong to the long-term observatory ORCHAMP (<www.orchamp.osug.fr>, Supplementary material Appendix 1) and were selected according to the following criteria: 1) continuous gradient from about 900 m to 3000 m (Supplementary material Appendix 1 Fig. A1-A), 2) exposure and slope along the gradient is homogeneous, 3) vegetation is typical for the elevation stages with forests dominating the lower parts and alpine meadows the higher parts of the gradient and 4) all gradients together are representative for the environmental

and topographical variability of the French Alps (Fig. 1, Supplementary material Appendix 1 Fig. A1-B). Between 2016 and 2018, a minimum of five sampling plots (30×30 m, see Fig. 1 for details) were installed along each elevation gradient, with an average of 200 m elevation difference, resulting in 99 plots in total (Supplementary material Appendix 1 Fig. A1). Each plot included a subplot for collecting plant data and three subplots for soil sampling (Fig. 1). Plant and soil data were always sampled in the same year. All plant species in the subplot were identified by professional botanists. For the analyses, we only kept the 44 species for which we had sufficient presences (i.e. > 20 plots, Supplementary material Appendix 2 Table A1) to build reliable species distribution models (Guisan et al. 2017). For each plant species, we selected plant height and three leaf traits, the ratio between leaf carbon and nitrogen contents (leaf C/N), leaf dry matter content (LDMC) and specific leaf area (SLA) because they represent important aspects of plant nutrition and light competition (Cornelissen et al. 2003). Traits were retrieved from our own trait database, and averaged at the species level. On average 10 individuals were sampled over different environmental conditions typical for the French Alps following standard protocols (Supplementary material Appendix 2 Table A1; Cornelissen et al. 2003).

Climatic data

To best characterize species' climatic niches, we calculated a set of bioclimatic variables as averages over 1988–2018. More specifically, we used solar radiation and growing degree days (GDD, Choler 2018) to represent the average length and intensity of the growing season, intensity of freezing events (freezing degree days, FDD, Choler 2018) and water stress (climatic water deficit, CWD) in each plot (see Table 1 for details). These variables were calculated from the SAFRAN-SURFEX/ISBA-Crocus-MEPRA reanalysis (Durand et al. 2009, Vannier 2012). This corresponds to a version almost identical to the dataset made available by Vernay et al. (2019). The last corrections made before the publication of

this dataset are sufficiently minor to not modify the conclusions of this study. A key advantage of this model is that it combines observed weather station data and the output of numerical weather prediction models, and provides a joint product addressing meteorological and snow conditions in mountainous regions, based on large-scale topographical features (e.g. elevation, slope, aspect). This is of particular importance in mountain environments, where the starting point and the length of the growing season is determined by the presence of snow (Choler 2005, Carlson et al. 2015).

Soil sampling, soil physico-chemical properties and exoenzymatic activities

We sampled soil in each of the three 2×2 m soil subplots located 5 m below the inner transect of each sampling plot (Fig. 1). In each subplot, we sampled ten soil cores (10 cm depth \times 5 cm diameter) and immediately pooled and homogenized them. We sieved the resulting composite samples with 5.6 mm-sieves. We froze 2.75 g per sample for subsequent exoenzyme analyses (soil sub-samples B), 5 g to quantify water content of each sample, and kept the rest for physico-chemical analyses (soil sub-samples A).

From soil sub-samples A, we measured pH, soil C/N, total nitrogen content, soil organic matter. These soil physico-chemical properties also represent long-term effects of plants on soils. For example, soil C/N, total nitrogen content and soil organic matter depend on the quantity and quality of the plant litter inputs, and top-soil pH is also determined by interactions with the plant rhizosphere. We first further homogenized, dried and 2 mm-sieved the soil. A part of the soil was grounded to a particle size below $250 \mu\text{m}$ with an ultra-centrifugal grinder ZM 200 (Retsch ZM200) to determine total soil carbon and nitrogen contents using an elementary analyzer (Flash EA1112, Thermo Scientific). We gently crushed the rest of the samples, measured pH following the ISO 10390:2005 norm using a pH-meter (pH7110, inoLab) in a 1/5 solution (1 volumic part soil sample and 4 volumic parts distilled water), and quantified soil moisture content (after drying a subsample at 70°C for

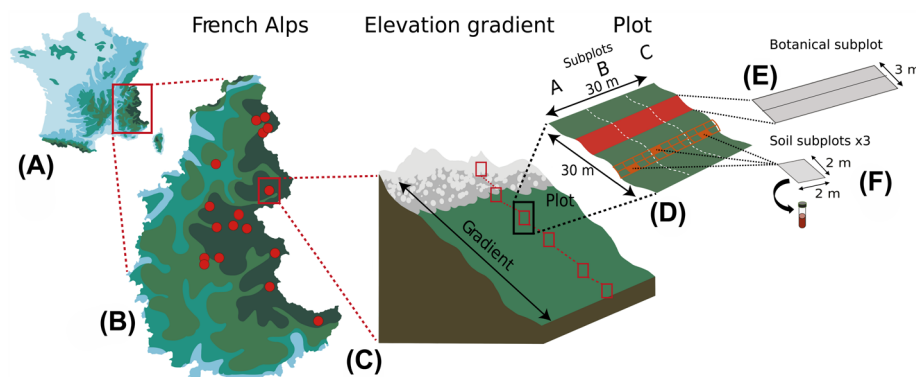


Figure 1. Experimental design of the ORCHAMP long-term observatory. (A) Location of the observatory in the French Alps, (B) location of the 18 elevation gradients, (C) example of the elevation distribution along the gradient, (D) sampling design of one plot. The inner transect (red area, E) represents the botanical sampling region, where all plants were identified. The squared zone (F) represents the area where the soil sampling is done on three 2×2 m subplots randomly chosen for each year of sampling.

Table 1. Climatic variables included in model 1 as a baseline of the forward stepwise selection. We extracted the raw meteorological and snow variables from the SAFRAN-SURFEX/Crocus-MEPRA reanalysis.

Name	Unit	Intermediate variables	Formula (one year)	Description and period
Growing degree days (GDD)	°C yr ⁻¹	Daily mean soil temperature at 10 cm depth (T_{avg_i})	$\sum_i T_{avg_i}$, with $T_{avg_i}=0$ if $T_{avg_i}<0$	Annual sum of average daily degrees above zero, averaged over 1988–2018.
Freezing degree days (FDD)	°C yr ⁻¹	Daily mean soil temperature at 10 cm depth (T_{avg_i})	$\sum_i T_{avg_i}$, with $T_{avg_i}=0$ if $T_{avg_i}>0$	Annual sum of average daily degrees below zero, averaged over 1988–2018.
Solar radiation	W m ⁻²	Daily surface incident direct shortwave radiation (DIR_SW_i), daily surface incident diffuse shortwave radiation (SCA_SW_i)	$\sum_i DIR_SW_i + SCA_SW_i$	Sum of daily solar radiation accumulated over the growing season, averaged over 1988–2018.
Climatic water deficit (CWD)	mm yr ⁻¹	Daily rainfall sum ($Psum_i$), daily reference evapotranspiration (ET_0) from daily wind speed, surface pressure, relative humidity and saturated water vapor pressure (Allen et al. 1998, Vannier 2012)	$\sum_i Psum_i - ET_0$, with $Psum_i - ET_0 = 0$ if $Psum_i - ET_0 > 0$	Sum of daily climatic water deficit: the sum of the negative daily climatic water balance, over the growing season, averaged over 1988–2018.

48 h) and organic matter (SOM) content by Loss on Ignition (after 4 h incubation in a muffle furnace at 550°C).

From soil sub-samples B, we estimated exoenzymatic activity of seven exoenzymes involved in the degradation of C-rich substrates (EEC: α -Glucosidase (AG), β -1,4-Glucosidase (BG), β -D-Cellobiosidase (CB) and β -Xylosidase (XYL)), N-rich substrates (EEN: β -1,4-N-acetylglucosaminidase (NAG) and leucine aminopeptidase) and P-rich substrates (phosphatase (PHOS)) using standardized fluorimetric techniques (Bell et al. 2013). We homogenized soil during 1 min in a Waring blender in 200 ml of a sodium acetate buffer solution. Then soil slurry was added in technical duplicates to a 96-deep-well microplate with 200 μ l of substrates specific to each enzyme at the saturation concentration. Exoenzymatic activities were assayed at pH 5 (mean pH across the sites, equivalent to meta-analysis from Sinsabaugh et al. 2008). For each soil sample duplicated standard curves were prepared by mixing 800 μ l of soil slurry with 200 μ l of 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (MUC) in 96-deep-well microplates with growing concentrations from 0 to 100 μ M concentration. Plates were incubated at 25°C in the dark (3 h) on a rotary shaker (150 rpm) before centrifugation at 2900 g (3 min). Finally, fluorescence was measured on 250 μ l of supernatant on a microplate reader (Varioscan Flash, Thermo Scientific) with excitation wavelength set to 365 nm and emission set to 450 nm. Exoenzymatic activities were expressed as nmol g soil⁻¹ h⁻¹, after correcting for negative controls. We calculated the total potential extracellular enzymatic activity (total EEA) as the sum of the potential enzymatic activities of the seven exoenzymes as well as the ratio of the potential activities of exoenzymes targeting nitrogen vs phosphorus (EEN/EEP), the relative potential activity of exoenzymes targeting nitrogen (EEN/total EEA) and phosphorus (EEP/total EEA, see Table 2 for details), respectively.

Statistical analyses

We aimed to build a model in which species traits can influence the species response to environmental variables. We did

so in two steps. First, we determined the shape of the species response to environmental variables using a flexible data-driven model (i.e. generalized mixed-effect additive model) and used a stepwise selection procedure to select the best set of variables. Second, with the selected environmental variables, and for each single trait, we built a final hierarchical species distribution model that includes species response to environment modulated by species traits.

Step 1 – selection of environmental variables and associated response shapes

Our list of environmental variables was initially as follows: climate (i.e. GDD, FDD, CWD, solar radiation), soil physico-chemical properties (i.e. soil C/N, pH, total nitrogen content, SOM) and microbial decomposition activity (i.e. total EEA, EEP/total EEA, EEN/total EEA, EEN/EEP). All variables were centered and scaled, while plant height was also log-transformed.

1) We removed variables that were too correlated using the ‘findCorrelation’ of the package ‘caret’ in R. If two variables are highly correlated, this function removes the variable with the highest mean absolute correlation. Average correlations are re-evaluated each time a variable is removed (Kuhn 2008). We also checked whether these choices made sense from an ecological point of view. SOM, EEN/EEP, CWD and solar radiation were dropped, in line with our expectations that they were moderately associated with plant species distributions (see Supplementary material Appendix 2 Fig. A3 for details).

2) To determine the shape of species response to environmental variables, we then used a generalized additive mixed-effect model (GAMM) with species identity as random effects. Only the plant response to GDD was clearly unimodal and therefore we included GDD as a squared term in the subsequent analyses (Supplementary material Appendix 2 Fig. A4).

3) To select the best combination of environmental variables, we then performed a forward selection using Bayesian information criteria (BIC). Since the final hierarchical model is

Table 2. Extracellular enzymatic activities (EEA) included in model 1 to perform a forward stepwise selection.

Name	Unit	Intermediate variables	Formula
Total potential exoenzymatic activity (total EEA), sum of all measured exoenzyme activities	nmol g ⁻¹ dry mass	α-Glucosidase (AG), β-glucosidase (BG), β-D-cellubiosidase (CB), β-xylosidase (XYL), leucine aminopeptidase (LAP), N-acetyl-β-glucosaminidase (NAG), phosphatase (PHOS)	Total EEA = AG + BG + CB + XYL + LAP + NAG + PHOS
Ratio of exoenzymes targeting nitrogen and phosphorus (EEN/EEP)	–	Exoenzymes targeting nitrogen: LAP and NAG. Exoenzyme targeting phosphorus: PHOS	$\frac{EEN}{EEP} = \frac{LAP + NAG}{PHOS}$
Relative activity of exoenzymes targeting nitrogen (EEN/total EEA)	–	Exoenzymes targeting nitrogen: LAP and NAG, total EEA	$\frac{EEN}{total\ EEA} = \frac{LAP + NAG}{total\ EEA}$
Relative activity of exoenzymes targeting phosphorus (EEP/total EEA)	–	Exoenzyme targeting phosphorus: PHOS, total EEA	$\frac{EEP}{total\ EEA} = \frac{PHOS}{total\ EEA}$

based on generalized linear mixed-effect models (GLMM), we here used a GLMM instead of a GAMM. The stepwise algorithm selection was constrained to stop for $\Delta BIC > 10$ or after six abiotic variables were included. We used the final model resulting of this selection procedure (model 1) as the basis for the subsequent analyses (models 2–5 including traits).

Step 2 – hierarchical species distribution models

From model 1, we built a hierarchical species distribution model for every single trait. That prevented us from model saturation. In other words, for leaf C/N (model 2), LDMC (model 3), plant height (model 4) and SLA (model 5), we modeled the probability of presence \mathbf{P} of species s , $s \in \{1 \dots 44\}$, at a site i , $i \in \{1 \dots 99\}$, as:

$$\text{logit}(\mathbf{P}_{s,i}) = \sum_{c=1}^6 B_{c,s} X_{c,i} + \gamma_s + \varepsilon_i$$

where the $X_{c,i}$ were the fixed environmental variable $c \in \{1 \dots 6\}$ at site i selected by model 1, γ_s was the random intercept for species identity, ε_i was a normally distributed error term. The $B_{c,s}$ parameters were modeled as:

$$B_{c,s} = \beta_{c,s} + \beta_{c,0} + \beta_{c,t} \times T_s$$

where $\beta_{c,s}$ is the random slope for species identity, $\beta_{c,0}$ can be interpreted as the coefficient for a hypothetical species with an average trait and $\beta_{c,t}$ described how trait T modulates the partial response of the species to the environmental variable X_c . In this paper, trait T was averaged at the species level. The interaction between the mean trait T and the environmental variable X_c provides information on how far the species is from its environmental optimum, and in that sense ‘modulates’ species probability of presence along environmental gradients. A positive trait–environment interaction (i.e. positive $\beta_{c,t}$) means that a species s with high trait value T_s has a high probability of presence (high $\mathbf{P}_{s,i}$) for a site i with high values of the considered environmental variable $X_{c,i}$.

The four hierarchical GLMMs were fitted using a binomial response and a logit link. Species identity was included as a random effect, for which both slope and intercept were allowed to vary.

Parameters of all models were estimated by Laplace approximation of maximum likelihood using the ‘Bobyga’ optimiser of the ‘lmer’ function (package ‘lme4’ in R, R Core Team). We ensured model convergence by prohibiting the estimation of the correlations between random effects.

Model evaluation

To evaluate the hierarchical GLMM, we calculated the true skill statistic (TSS), which has the advantage to account both for the model sensitivity (i.e. proportion of observed presences predicted as presences) and specificity (i.e. the proportion of observed absences predicted as absences, Allouche et al. 2006). TSS can vary from -1 to 1 , where $+1$ indicates perfect fit and values of zero or less indicate a performance no better or worse than random (Allouche et al. 2006). We also calculated TSS values per species. Since the TSS requires a threshold to transform species’ probability of presence into binary presence–absence data, we selected the threshold that maximizes the TSS values.

Results

Relative roles of climate, soil physico-chemical properties and microbial decomposition activity on plant distributions

The most parsimonious GLMM model identified with the stepwise selection procedure had a good predictive accuracy and included a single climatic variable together with three soil variables (TSS = 0.436, model 1; Fig. 2).

Overall, soil properties were key to predict plant distributions. Soil C/N, a proxy for organic matter decomposability, had the strongest impact on plant presence, followed by growing degree days (GDD²), pH and total EEA. Across

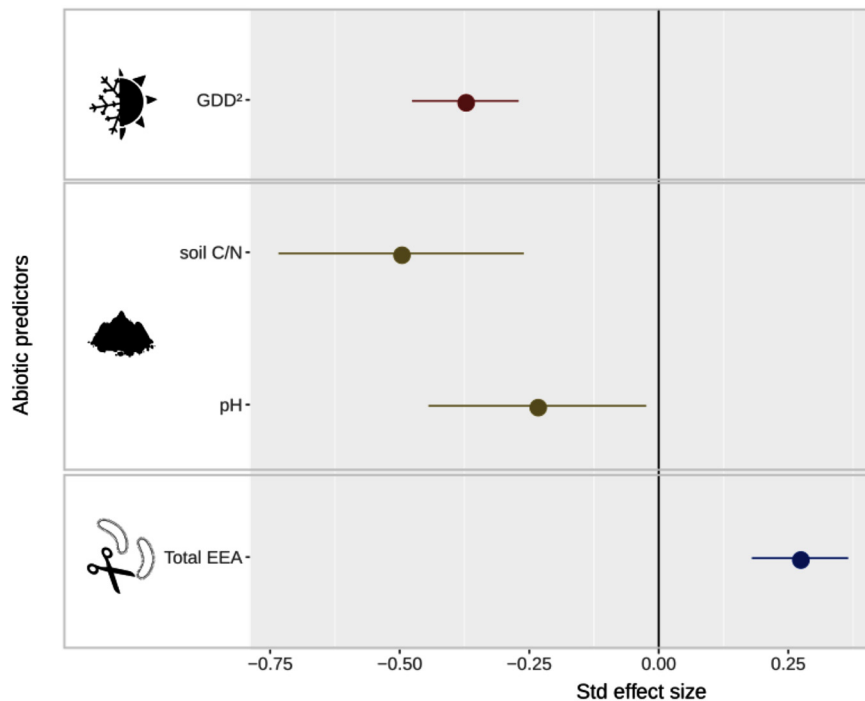


Figure 2. Estimated standardized effect sizes of the environmental variables selected by the stepwise procedure using BIC (model 1). Red, green and blue points represent environmental variables related to climate, soil physico-chemical properties and exoenzymatic activities, respectively.

species, probability of plant presence was highest for low C/N, low pH, high total EEA and intermediate values of GDD (model 1, Fig. 2).

Species with different functional traits respond differently to gradients of soil properties

In general, both model 1 (GLMM without traits) and the hierarchical trait-based GLMM models 2–5 (hierarchical trait-based GLMM) had good predictive accuracy for most species (average TSS=0.46; Supplementary material Appendix 2 Fig. A5). Only three species had a TSS score lower than 0.3. Models accounting for functional traits (models 2, 3, 4=0.440, model 5=0.444) were slightly better than the model accounting for the environment only (model 1, TSS=0.436).

Plant species showed different responses to the environment and notably a strong trade-off along the gradients of two soil characteristics (model 1, Fig. 3): Some species were more generally found under a combination of low soil C/N and high total EEA, while others were more common under a combination of high soil C/N and low total EEA. This trade-off was not due to a sampling bias since the two gradients were independent in our study area (i.e. low correlation of soil C/N and EEA over all plots; Supplementary material Appendix 2 Fig. A3).

Species-specific responses could be partially related to their functional traits. Species with conservative traits (high leaf C/N, high LDMC) were favored where organic matter

was hard to decompose (high soil C/N, Fig. 3, 4, models 2, 3). Furthermore, smaller species preferred low C/N and high total EEA sites (Fig. 3, 4, model 4). All plants benefited from microbial decomposition activity (high total EEA) but especially small species were favored on soils with high nutrient availability. Interestingly, no functional trait modulated species responses to pH or GDD (models 2, 3, 4, 5), but variability between species responses to the GDD gradient was also much lower compared to the variability along gradients of soil properties (Fig. 3, Supplementary material Appendix 2 Fig. A6-A).

Discussion

Understanding the mechanisms underlying plant distributions is a great challenge to anticipate the consequences of global changes on plant communities (Thuiller et al. 2008). Here, we develop a multi-species distribution model first to test how soil properties, especially microbial decomposition activities, shape plant species distributions in mountain environments, and second to account for how functional traits modulate species response to environmental gradients. We find that top-soil properties linked to nutrient recycling (microbial decomposition activity and organic matter decomposability) play a key role regarding plant distributions. Furthermore, we show that functional traits of plants related to resource acquisition strategies modulate plant response to soil properties. Exploitative species with

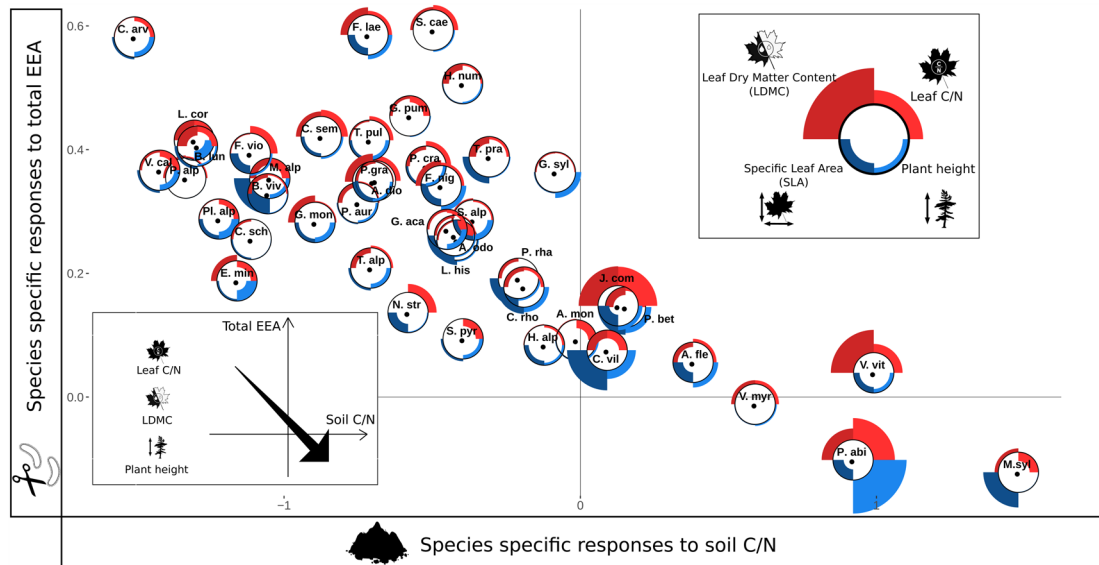


Figure 3. Species-specific partial response to total EEA as a function of species-specific partial response to soil C/N. Pie-charts represent the functional trait values of the species. The red and blue traits are expected to modulate the species response to soil properties and climate, respectively. The right-up box is a species (*Vaccinium vitis-idaea*) example with the legend for the functional traits. The left-bottom box shows the direction of increase for plant height, LDMC and leaf C/N. Full species names are given in Supplementary material Appendix 2 Table A1.

acquisitive functional traits (e.g. low leaf C/N, low LDMC) are favored on soils with quick nutrient recycling, while conservative species (e.g. woody, with high leaf C/N and LDMC) dominate on nutrient-poor soils. In line with the 'fast-slow' plant economics spectrum (Reich 2014), we show that the spatial segregation of ecological strategies following top-soil properties helps to explain mountain plant distributions along elevational gradients.

Relative roles of climate, soil physico-chemical properties and microbial decomposition activity in explaining plant distributions in mountain ecosystems

Climate remained an important driver of plant distributions in our mountain system. Species probability of presence was maximized for intermediate values of GDD (model 1, Fig. 2). This was expected, given the importance of the length and intensity of the growing season for mountain plants (Körner 2003, Choler 2018). Interestingly, we show that top-soil properties play a key role for plant distributions, with an explanatory power comparable to that of climate. Increasing pH decreased the probability of presence of plant species (model 1, Fig. 2). In the literature, pH is consistently reported to be an important driver of plant distributions. Its influence is possibly due to the switch from calcareous to siliceous bedrock, for which plants are specialized or not (Lee 1998, Corlett and Tomlinson 2020). Given that we measured pH on the first horizon, its influence might also be related to the interplay between plant litter, rhizosphere and soil physico-chemical properties, which affects microbial communities and nutrient supply to plants (Smiley 1974, Wang and Tang 2018).

Our study demonstrates that soil properties associated with nutrient availability are tightly associated with plant species distributions. Overall, species presence probabilities increased in nutrient-rich conditions, such as those indicated by high microbial decomposition activity and organic matter of high quality (i.e. high total EEA and low soil C/N, Fig. 3, 4). Some studies found a significant effect of soil C/N on trees and woody species (e.g. positive on ericaceous as *Vaccinium myrtillus*, Coudun and Gégout 2007, Walthert and Meier 2017), while others found weak effects on grassland plants (Dubuis et al. 2013, Buri et al. 2017). The varied effects of soil C/N were explained by the fact that measures of soil nutrient pools do not give information on the decomposition of the molecules involved (Dubuis et al. 2013, Buri et al. 2017). In mountain areas, soil C/N might be low although organic pools of nitrogen are tied up with soil organic matter as complex insoluble polymers that are not accessible to plants (Wardle and Bardgett 2002, Körner 2003, Buri et al. 2017). However, our results show that combining soil C/N as a measure of organic matter decomposability and total EEA as measure of the microbial decomposition activity improves the representation of nutrients available to plants both in forests and in grasslands and thus our capacity to predict plant distributions (Fig. 3).

Species with different functional traits respond differently to gradients of soil properties

Although all species respond positively to favorable environmental conditions, especially exploitative plants were advantaged in nutrient-rich places with mild climate. Under these favorable conditions, conservative species bear the costs of

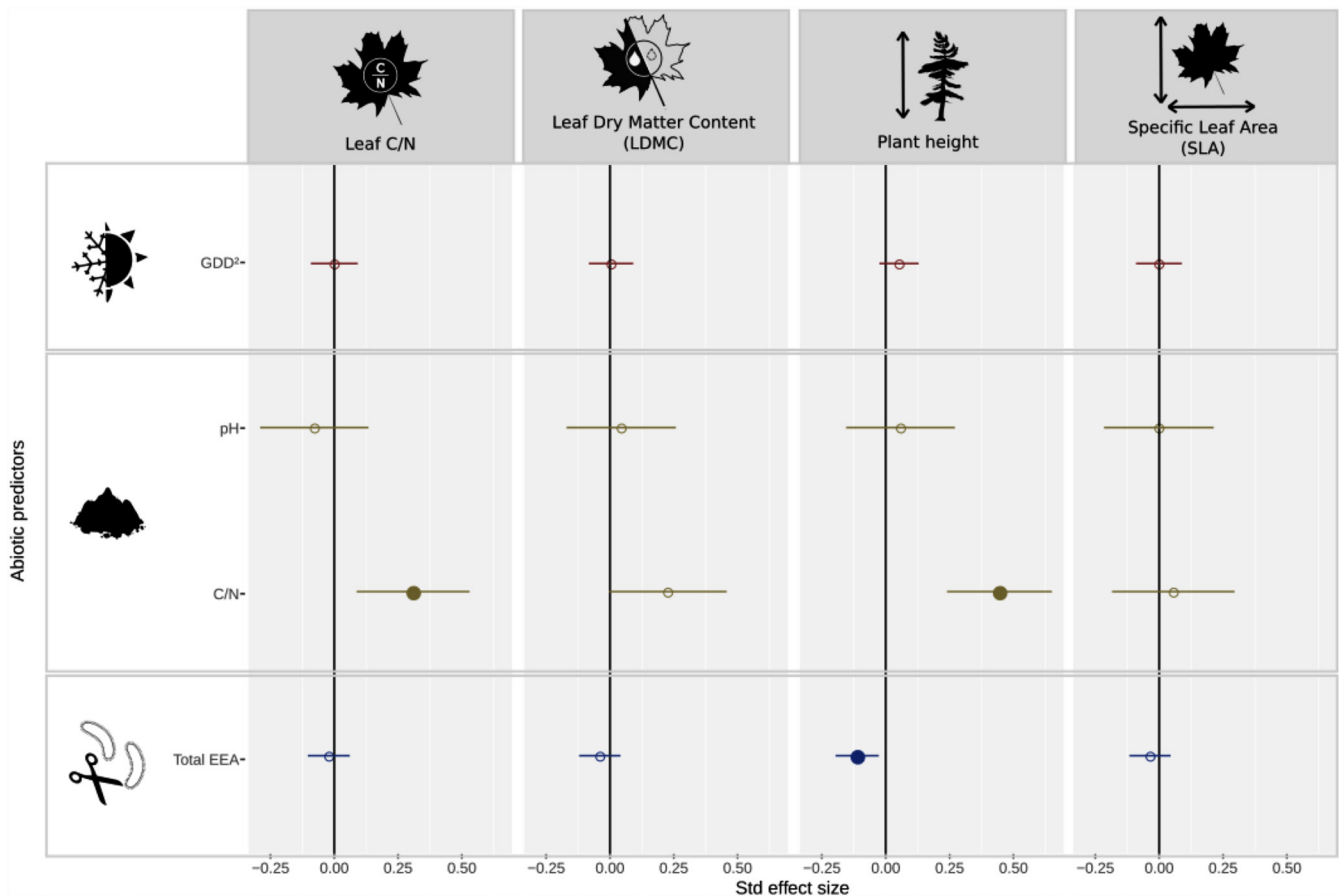


Figure 4. Estimated standardized effect sizes of the interaction between functional traits (leaf C/N, model 2; LDMC, model 3; plant height, model 4; specific leaf area; model 5) and environmental variables. Contrasting rows for a single column allow comparing the modulating effect of the different functional traits for a single environmental variable. Filled and open circles represent significant and non-significant effects, respectively. Red, green and blue points represent environmental variables related to climate, soil physico-chemical properties and exoenzymatic activities, respectively.

being excluded by plants with a more exploitative strategy (mostly herbaceous species, Fig. 3, Supplementary material Appendix 2 Fig. A6-7). Surprisingly, while we expected traits related to light competition (i.e. tall plants with high SLA) to confer a particular advantage to plants under mild environmental conditions, we found no significant modulating effect of SLA for any of the environmental axes, and height conferred an advantage rather on nutrient-poorer soils. This is in opposition to the literature on broader grassland types (Pollock et al. 2012, Carboni et al. 2018), but can be due to the fact that alpine plants are overall selected for rather small sizes and a small range of SLA to resist to cold temperatures (Körner 2003). The advantage for tall plants on nutrient-poorer soils is due to the fact that within our dataset those plants were mostly woody species with a slower growth rate (*Juniperus communis*, *Vaccinium myrtillus*, *Picea abies*, *Vaccinium vitis-idaea*, Fig. 3, Supplementary material Appendix 2 Fig. A7).

In our alpine study, the variability among the responses of species along the gradient of soil properties was bigger than along the climatic gradient (Supplementary material Appendix 2 Fig. A6), which could suggest that spatial

segregation of plants with different strategies was mostly driven by soil properties (Reich 2014). Although the probability of presence of most plants increased in places with high soil organic matter decomposability (low soil C/N), the probability of presence of some species increased on nutrient-poor soils (e.g. woody species, Fig. 3, Supplementary material Appendix 2 Fig. A6-7), reflecting a differentiated strategy with selection for conservative traits, i.e. higher leaf C/N and LDMC (Fig. 4, Supplementary material Appendix 2 Fig. A7). Conservative leaf traits are necessary on nutrient-poorer soils with high soil C/N and give an advantage reinforced by plant-soil feedbacks (Aerts 1995, Reich 2014). Leaves with higher C/N contribute to the low decomposability level of the soil organic matter, which slows down decomposition, and reinforces high soil C/N (Grigulis et al. 2013, Legay et al. 2016). This confirms the hypothesis of Aerts (1999), which states that in nutrient-poor habitats, selection is based more on the ability of plants to limit nutrient losses than on their ability to access nutrients quickly.

Although our results suggest that exploitative plants are often excluded as a result of strong nutrient limitations of

mountain soils, nutrients such as nitrogen are not only supplied to plants from the decomposition of soil organic matter. With the continuous increase of atmospheric nitrogen deposition since the industrial age (Galloway et al. 2008), nitrogen limitation might become less problematic in the future. Associated with milder temperatures, increased atmospheric nitrogen depositions in mountain areas could result in a shift towards communities dominated by exploitative plants and the competitive exclusion of conservative ones (Hautier et al. 2009, Boutin et al. 2017). As plants with exploitative traits produce a litter easier to decompose, these community shifts might drive accelerated nutrient cycling rates in alpine systems, with unknown consequences on the carbon and nitrogen cycles at larger scales.

Finally, we used the mean of traits measured at different places, mostly in the French Alps, which represents the mean habitat suitability of the modeled species (Albert et al. 2012). However, within species, plants also respond to gradients of climatic and soil properties through modifications of the values of response traits by phenotypic plasticity or local adaptation (Lavorel and Garnier 2002). It has been shown that these variations around the mean traits influence the relationships of diversity measures with environmental gradients (Albert et al. 2012), and that intra-specific trait variability influences species distributions at small scales in alpine systems (Chalmandrier et al. 2017). We might thus expect that intra-specific trait distributions would influence our trait-based distribution models. For example, it might reinforce the importance of traits–environment interactions or improve the explanatory power of trait-based species distribution models by providing information at finer scale for each species. In that sense, accounting for intraspecific trait variability is an interesting perspective of trait-based species distribution models.

To conclude, by bridging soil biogeochemistry and plant biogeography we provide novel insights on how soil properties linked to nutrient availability shape mountain plant distributions in addition to climate. We show that incorporating microbial decomposition activity improves plant distribution models, probably because it allows estimating plant nutrient supply. Finally, our results support our hypothesis that plant functional traits associated with conservative–exploitative strategies modulate distributions along gradients of top-soil properties associated with nutrient availability. Future prospects include a better understanding of the influence of the interaction between climate change and atmospheric nitrogen deposition on plants and the inclusion of intraspecific trait variability in large-scale distribution models.

Data availability statement

Most of the raw data used in the manuscript are directly available on the ORCHAMP website (<<https://orchamp.osug.fr/home>>). The data supporting the results are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.2z34tmpjg>> (Martinez-Almoyna et al. 2020).

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Authors contributions – CMA, TM and WT conceptualized the overall study and analyses. WT, AS, CMA, TM and the ORCHAMP Consortium collected the soil data. LB carried out the plant trait measurements. JR run the database and formatted the climate data. GP, LB and AS carried out the lab work for exoenzymatic activities and soil properties. CMA run all statistical analyses. CMA, TM and WT led the interpretation of the results with strong support from GB, PC, JP and AF. CMA led the writing with contributions of all authors.

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Supplementary material (available online as Appendix ecog-05269 at <www.ecography.org/appendix/ecog-05269>). Appendix 1–2.

Du chapitre 3 au chapitre 4 ...

Dans le troisième chapitre, nous avons montré que l'activité de décomposition microbienne joue un rôle primordial pour structurer les distributions des espèces de plantes le long de plusieurs gradients d'altitude dans les Alpes, alors que les traits de la communauté microbienne, liés à leur investissement pour l'acquisition de différents nutriments, n'influencent pas significativement les distributions des plantes. Ce résultat met en évidence le fait que la composition de certains groupes trophiques (ex. les plantes) peut être influencée par les fonctions écosystémiques (ex. la décomposition) principalement portées par d'autres groupes trophiques (ex. les bactéries et les champignons), et soulève la question des boucles de rétroactions entre les fonctions écosystémiques et la composition des différents groupes trophiques, ainsi qu'entre différentes fonctions écosystémiques.

Dans un quatrième chapitre, issu de la thèse de master 2 de Sarah-Sophie Weil, nous adoptons une démarche exploratoire et non-dirigée pour démêler les associations dans l'espace géographique entre traits et fonction des communautés microbiennes, et traits et fonction des communautés de plantes.

Ce chapitre est présenté en anglais. Il est actuellement en révisions majeures et formaté pour *Journal of Biogeography*.

Chapitre 4, Strong links between plant traits and microbial activities but different abiotic drivers in mountain grasslands

Short running title: Plant-soil relationships in mountains



Identifying plants on the last plot of the Lauvitel gradient (RBI)

Sarah-Sophie Weil¹, Camille Martinez-Almoyna¹, Gabin Piton¹, Julien Renaud¹, Louise Boulangeat¹, Arnaud Foulquier¹, Amélie Saillard¹, Philippe Choler¹, Jérôme Poulencard², The ORCHAMP consortium, Tamara Münkemüller¹ and Wilfried Thuiller¹

¹Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, F-38000, Grenoble, France

²Univ. Savoie Mont Blanc, Univ. Grenoble Alpes, CNRS, EDYTEM, F-73000, Chambéry, France

Keywords: elevational gradient, graphical lasso, ORCHAMP, partial correlation network, plant functional traits, plant-soil linkages, soil enzymatic activities

ABSTRACT

Aim: Plant-soil interactions can be major driving forces of community responses to environmental changes in terrestrial ecosystems. These interactions can leave signals in aboveground plant functional traits and belowground microbial activities which manifest in observed covariations. However, we know little about how these plant-soil linkages vary in response to environmental conditions at biogeographic scales for which experiments are impossible. Here, we investigate across the French Alps patterns of direct and indirect linkages between plant functional traits, soil microbial activities and environmental conditions in mountain grasslands along elevational gradients.

Location: The French Alps.

Taxon: Vascular plants and soil microbiota.

Methods: We analyzed observational grassland data sampled along 14 elevational gradients across the entire French Alps (between 1500 and 2800m of elevation). Using Graphical Lasso, we inferred a partial correlation network to tease apart direct and indirect plant-soil linkages without defining the direction of interactions a priori.

Results: We found tight spatial associations of plant traits with microbial activities, climate driving the former and soil properties the latter. In these plant-soil linkages, the dominance of specific plant traits was more important than their diversity. We then showed that in sites with conservative plant traits and reduced organic matter quality, soil microbes invested strongly in nutrient acquisition.

Main conclusions: By investigating plant-soil linkages along elevational gradients in the French Alps, we showed that plant functional traits and belowground microbial activity are tightly linked and how they depend on environmental conditions. Overall, we demonstrated how soil functioning can be integrated in studies of ecosystem shifts under environmental change at large spatial scales.

INTRODUCTION

Plant-soil interactions are fundamental elements of ecosystem functioning and structure (Wardle *et al.*, 2004; Bardgett & Wardle, 2010; de Vries *et al.*, 2013; Martinez-Almoyna *et al.*, 2019). Plants rely on soil microbial communities that drive decomposition of detrital organic matter and the recycling of nutrients through their extracellular enzymatic activities (Burns & Dick, 2002; Schimel & Bennet, 2004; Burns *et al.*, 2013). Conversely, the resource-acquisition strategy of soil microbes depends on the quantity and nutritional quality of plant litter inputs, and is reflected in the relative investment in extracellular enzymes that target C-, N- or P-rich compounds (Bowman, Steltzer, Rosenstiel, Cleveland & Meier, 2004; Bardgett & Wardle, 2010; Fanin, Hättenschwiler & Fromin, 2014; Legay *et al.*, 2014; Piton, Legay, *et al.*, 2020).

Observed correlations between components of plant communities and soil microbial communities, called plant-soil linkages in the following, can be the result of plants affecting soil, of soil affecting plants, or of both processes simultaneously (Fig. 1). Concerning the effect of plants on soil ecosystem properties, there are two conflicting visions in the literature. Grime (1998; see also García-Palacios, Shaw, Wall & Hättenschwiler, 2017) proposed that plant species in a community control ecosystem functions, such as primary production, resistance and resilience to perturbations and nutrient cycling and storage, proportionally to their biomass. In other words, the traits of dominant plant species determine ecosystem properties more strongly than the traits of rare species (*mass-ratio-hypothesis*). On the other hand, it was suggested that functional diversity affects ecosystem functioning through complementary use of resources (*diversity-function-hypothesis*; Tilman *et al.*, 1997; Hooper *et al.*, 2005). For example, diverse plant communities may increase rates of nitrogen (N) cycling by providing variable litter qualities that can be broken down at different rates, thus providing a more consistent supply of organic N (Laughlin, 2011). Since rare species can have keystone effects and strongly influence pathways of energy and material flows (see also Violle *et al.*, 2017), the relative abundance of species is not always a good predictor of ecosystem-level importance of species. These hypotheses have mostly been tested at regional scales for individual ecosystem processes, and most studies supported the *mass-ratio-hypothesis* (Díaz *et al.*, 2007; Grigulis *et al.*, 2013; Lavorel, 2013; García-Palacios *et al.*, 2017). However, we still lack knowledge about whether functional diversity or traits of dominant species are of greater importance in plant-soil linkages at biogeographic scales.

Soil functioning also impacts the plant community. On fertile soils with high nutrient availability, plant communities are often composed of exploitative plants (high leaf nitrogen content and low leaf dry matter content) and are associated with bacteria-dominated belowground communities that quickly decompose the easily degradable litter (Wardle *et al.*, 2004; Queded, Eriksson, Fortunel & Garnier, 2007; Fortunel *et al.*, 2009). On infertile soils with low nutrient availability, conservative plant communities with slow growth rates are often linked to fungi-dominated belowground communities with slower cycling rates but with the ability to decompose more recalcitrant material (Aerts, 1999; Bardgett & Wardle, 2010). Although these associations are well-known locally, at biogeographic scales it is rarely studied how the changes in nutrient and energy availability in soils influence the traits of plant communities along the exploitative to conservative plant spectrum (Piton, Legay, *et al.*, 2020).

Extracellular enzymatic activities (EEAs) of microbial communities are related to both nutrient availability and microbial growth, acting at the interface between aboveground and belowground communities. EEAs can be either directed towards nutrient (e.g. N or P) or energy (i.e. C) acquisition. Ratios of EEAs therefore reflect the equilibria between elemental composition of microbial biomass and soil organic matter (Sinsabaugh, Hill & Shah, 2009), and the shift between nutrient and energy flow associated with microbial community metabolism. Although EEAs might underlie plant-soil linkages through organic matter recycling, their relationship with plant traits have rarely been investigated.

On top of plant-soil interactions, environmental conditions, i.e. soil physicochemical properties and climate, also influence the plant and microbial communities differentially, and therefore modulate their observed linkages (Bonito *et al.*, 2014; Van der Putten, Bradford, Brinkman, van de Voorde & Veen, 2016, Fig. 1). In mountain systems, for instance, temperature and snow cover determine growing season length, solar radiation that plants are exposed to, soil moisture regime and soil pH. These environmental conditions might affect nutrient and energy availability which impacts soil microbial communities, EEAs, plant community composition, and associated litter quality, and in turn, nutrient availability. In particular, freezing cycles constitute a physiological stress which alters microbial demand and allocation of C and nutrients (Freppaz, Williams, Edwards, Scalenghe & Zanini, 2007; Schimel, Balsler & Wallenstein, 2007). However, it is difficult to distinguish between direct and cascading effects of the environment on plant-soil linkages because of the multitude of interactions between all components of the system. This is why all components implicated in the complex system of plant-soil linkages have rarely been studied together in the past (e.g. Wardle *et al.*, 2004; Kulmatiski, Beard, Stevens & Cobbold, 2008; Delgado-Baquerizo *et al.*, 2019).

At biogeographic scales, it is almost impossible to uncover and study interactions through experiments. But plant-soil interactions leave correlative signals in spatial patterns of aboveground functional traits and belowground activity that we can study with observational data (de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2018). We know, for instance, that at large scales aboveground plant properties (e.g. exploitative-conservative spectrum) are drivers of soil microbial community diversity and composition (de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2018; Boeddinghaus *et al.*, 2019). In this context, especially abundance weighted trait values were used, but plant functional diversity was rarely assessed. Moreover, most models used in previous studies to infer patterns in aboveground-belowground linkages, such as structural equation models, assume causality and directionality. In particular, microbial community composition was mostly assumed to be the response variable (de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2018; Boeddinghaus *et al.*, 2019; but see Martinez-Almoyna *et al.*, 2020). However, aboveground-belowground linkages result from interactions and feedbacks. From observations alone, we can neither determine how the observed patterns were created nor the most prominent directions of the effects. They may result from plant traits influencing the soil community through litter quality, or from the soil community influencing the plant community through nutrient availability, or they may result from a combination of both. Also, we do not know where abiotic factors come into play and it is difficult to disentangle direct and indirect effects.

For these reasons, here, we propose to use graphical models to tease apart direct and indirect influences in plant-soil linkages without defining the direction of interactions a priori. Using a graphical lasso to infer a partial correlation network, we analyze interdependencies between aboveground plant functional traits, belowground enzymatic activities and abiotic conditions. We apply this method to grassland communities sampled along 14 elevational gradients from a large-scale observatory representative of the entire French Alps (ORCHAMP). Elevational gradients are associated with drastic abiotic gradients over short distances and are excellent systems to study ecosystem processes for a multitude of climatic and edaphic conditions, and to test how ecosystems respond to environmental variation (Sundqvist, Sanders & Wardle, 2013; Martinez-Almoyna *et al.*, 2019). We focus on mountain grasslands because little is known about large scale patterns in aboveground-belowground linkages in these vulnerable ecosystems. In the context of unprecedented environmental changes, understanding the relevance of plant-soil linkages for biogeographic distributions of plant diversity and microbial activity, and measuring the effects of single components on overall plant-soil functioning is of tremendous importance (Hagedorn, Gavazov & Alexander, 2019).

To better characterize plant-soil linkages along climatic and edaphic gradients in the French Alps, we ask three specific questions:

- (1) What is the importance of general abiotic and biotic interdependencies at biogeographic scales between four aspects of the plant-soil system – aboveground community (characterized by plant trait composition), belowground community (characterized through soil enzymatic activities), abiotic soil conditions, and climate?
- (2) Does functional diversity of plants or do functional traits of dominant species play a bigger role in plant-soil linkages?
- (3) Which specific associations exist between extracellular enzyme activities and other actors involved in plant-soil linkages?

MATERIALS & METHODS

Study area and the observatory ORCHAMP

ORCHAMP (Spatio-temporal observatory of biodiversity and ecosystem functioning of mountain socio-ecosystems, Supp. Mat.) is a long-term observation network covering the French Alps (Fig. 2, Fig. S1). It consists of multiple elevational gradients across the entire study area. For each gradient, 30m x 30m permanent plots were established every ~200m of altitude. Plant community releves (presence/absence and abundances), microbial activities, climatic conditions and soil properties were measured between 2016 and 2018 (Fig. S2). For this study, we selected 41 plots in open habitat (including grasslands and few shrublands) along 14 elevational gradients on different metamorphic and sedimentary bedrock, such as schist, gneiss and limestone (Fig. 2, complete sampling protocols and descriptions of the plots available on orchamp.osug.fr). Plant functional trait information comes from our own database and was sampled in the whole French Alps between 2008 and 2018 (see next section for details).

Biotic plant-soil linkages – Aboveground community

In each plot, we recorded plant species abundances using a pin-point sampling along a 30m transect parallel to the slope in the middle of the plot. Two measurements were taken every 20cm: one measurement 25cm upslope, the other 25cm downslope from the transect. All individuals touching the pole that marked the two measure points per 20cm increment were identified and counted. Furthermore, an additional dataset of presence/absences of all species along the same 30m transect but of 3m width was sampled to obtain a value of species richness representative of the whole plot. All plant species in the subplot were identified by professional botanists.

To test the mass-ratio-hypothesis (Grime, 1998), we calculated community-weighted means (CWMs) of plant traits (Garnier *et al.*, 2004; Lavorel *et al.*, 2008, Eq. 1).

$$(1) \quad \text{CWM} = \sum_{i=1}^n (p_i * \text{trait}_i)$$

where p_i is the relative abundance of species i in a plot, trait_i the trait value of species i and n the number of species.

We calculated the CWMs for the following traits: Leaf nitrogen content (LNC), leaf carbon to nitrogen ratio (C/N), leaf dry mass per area (LMA), leaf dry matter content (LDMC), plant height and root depth (RD). These traits were not measured on individuals on the Orchamp plots but in multiple populations across the whole French Alps to account for intra-specific variability (Albert, Thuiller, Yoccoz, Soudant, *et al.*, 2010) during the last ten years of field sampling. More specifically, at least 20 individuals were measured for traits related to height (vegetative and reproductive plant height) and 10 for leaf traits (LNC, C/N, LMA and LDMC). The measurements were carried out according to the protocol developed by Cornelissen *et al.* (2003). We used Flora indicativa (Landolt *et al.*, 2010) to complement missing data on vegetative and reproductive plant height, and to extract data on root depth (RD). Leaf carbon and nitrogen contents were measured with an elemental analyzer (Flash EA1112; Thermo Scientific). Mean trait values per species were then calculated.

In the 41 selected Orchamp plots, 484 different plant species were identified in total. On average, trait data was available for 82% of all individuals present in a given plot. They were transformed to approximate a normal distribution: a natural logarithm was applied to LNC and plant height, LDMC was square-root transformed and LMA, C/N and RD were logged (basis 10).

To measure the overall functional diversity of the plot, we calculated three independent measures: Functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) (Villéger, Mason & Mouillot, 2008). FRic represents the multidimensional volume of traits (trait space) filled by the species present in the community. For a single trait, this is simply the range of trait values spanned by the species present in the community. FDiv describes the overall functional divergence between species in the community. Low FDiv values mean that species within the community have similar combination of traits, thought to be indicative of strong environmental filtering (Mouchet, Villéger, Mason & Mouillot, 2010) but also asymmetric competition (Mayfield & Levine 2010). Reversely, high FDiv values indicate that species in the community have a wide range of trait values, leading to a high degree of complementarity and resource use. FEve measures the evenness in the distribution of abundances in trait space. In other words, whether species' abundances tend to be more abundant on one side (low complementarity) or to be evenly distributed in the trait space indicating a high degree of complementarity or niche partitioning among coexisting species. We included all six traits presented above to calculate the diversity measures using the R package "FD" (Laliberté *et al.*, 2014). The traits were standardised (mean $\mu=0$, standard deviation $\sigma=1$) before calculating FRic, FDiv and FEve. Since FRic and species richness were correlated (Villéger *et al.*, 2008; Pearson correlation between FRic and species richness > 0.98), we used a randomisation process and calculated the standard effect size to remove the effect of richness (FRic_ses; Supp. Mat., Pearson correlation between FRic_ses and species richness < 0.5).

The normalized difference vegetation index (NDVI) has been shown to be related to chlorophyll abundance and leaf area index (Myneni, Hall, Sellers & Marshak, 1995). We used the mean yearly sum of NDVI greater than 0.2 of the period 2000-2018 (NDVIint) as a proxy of plant primary productivity. Estimates of the surface spectral reflectance at a resolution of 250 m were derived from MODIS (Moderate Resolution Imaging Spectroradiometer) bands 1 and 2; MOD09Q1: MODIS/Terra Surface Reflectance 8-Day L3 Global 250m SIN Grid V006 satellite MODIS (Terra), available online: <https://lpdaac.usgs.gov/products/mod09q1v006/>. The preprocessing of NDVI time series followed the method described by Choler (2015).

Biotic plant-soil linkages– Belowground community

At 5m downside of the vegetation transect in each plot, soil samples were taken in three 2x2m sub-plots. In each subplot, repeated soil cores were taken from the top-soil (0-7cm depth) and mixed to get around 1kg of soil.

The collected composite samples were sieved at 5.6mm, and 40-50ml per sample were extracted and frozen at -20°C for subsequent analysis of microbial activities. The potential activities of seven different extracellular enzymes involved in carbon (α -Glucosidase (AG), β -Glucosidase

(BG), β -D-cellobiosidase (CB), β -Xylosidase (XYL)), nitrogen (Leucine aminopeptidase (LAP), N-acetyl- β -Glucosaminidase (NAG)) and phosphorus (Phosphatase (PHOS)) acquisition, were measured according to an adapted protocol of Bell *et al.* (2013) (see Supp. Mat.). The sum of all measured potential enzymatic activities (total EEA) was used as an overall indicator for the potential of the soil to depolymerize and recycle organic compounds and is therefore an important component of plant-soil linkages (Piton, Legay, *et al.*, 2020). Soil microbial community is the primary driver of this potential activity as microbes produce most of these enzymes. Then, abiotic factors (e.g. temperature) and processes (e.g. substrate diffusion and enzyme stabilisation in the soil matrix) modulate potential and realized enzymatic activity in situ (Wallenstein and Weintraub, 2008; Nannipieri, Trasar-Cepeda & Dick, 2018; Piton, Foulquier, *et al.*, 2020).

Enzyme activity vectors have recently been shown to quantify simultaneous resource demands of the belowground community and the belowground community's relative investment in C, N and P acquisition (Fanin, Moorhead & Bertrand, 2016; Moorhead, Sinsabaugh, Hill & Weintraub, 2016; Chen *et al.*, 2018). The proportional activity of enzymes targeting carbon (AG, BG, CB and XYL) and nitrogen (LAP and NAG) - i.e. $(AG+BG+CB+XYL)/[(AG+BG+CB+XYL)+(LAP+NAG)]$ - was plotted against C vs. P acquiring enzymes (PHOS) - i.e. $(AG+BG+CB+XYL)/[(AG+BG+CB+XYL)+(PHOS)]$. In general, a relative increase in the activity of enzymes targeting a specific element indicates that this element is limited in the environment (Olander & Vitousek, 2000). The length of the vector created by each point in the plot and the origin quantifies therefore relative C vs. nutrient limitation, with increasing vector length indicating increasing C limitation. The angle formed by the x-axis and the vector on the other hand quantifies the relative P vs. N limitation (Supp. Mat., Fig. S3). The three replicates of each plot were averaged, and a natural logarithm was applied to total EEA.

Abiotic factors modulating plant-soil linkages – Soil physicochemical properties

Soil dry weight was measured by weighing soil samples after drying at 70°C for 48h, and soil organic matter (SOM) was determined by loss on ignition using the previously dried samples (4h at 550°C).

The rest of the composite samples was then dried, sieved at 2mm and homogenised to obtain representative subsamples for the following analyses. We measured pH following the ISO 10390:2005 norm using a pH-meter (pH7110, inoLab) in a 1:5 soil/distilled water-solution. We used an Ultra Centrifugal Mill ZM 200 (Retsch ZM200) to grind part of the dried and sieved samples below 250 μ m. Carbon and nitrogen contents were then determined using an elemental analyser (Flash EA1112, Thermo Scientific). The three replicates per plot were averaged and SOM and C/N log-transformed.

Abiotic factors modulating plant-soil linkages – Climate variables

We characterized climate conditions at each plot using: Mean annual soil temperature (MAT), mean total annual precipitation (MAP), growing degree days (GDD), freezing degree days

(FDD), climate water stress (CWS) and solar radiation (SR). To do this, we extracted for each plot meteorological time series of surface conditions from the SAFRAN-Crocus (S2M) reanalyses that are available at hourly resolution for the time period 1988-2018 (Durand, Giraud *et al.*, 2009; Durand, Laternser *et al.*, 2009; Vionnet *et al.*, 2012; Vernay *et al.*, 2019). S2M is a regional-scale re-analysis that takes topographical effects into account. Data are produced for 23 massifs of the French Alps as a function of elevation in 300m increments, slope aspects and angles. The S2M reanalysis has been used for many real-time and climatological applications in the French mountain areas (e.g. Corona, Morin & Choler, 2018; Verfaillie *et al.*, 2018; see also Fig. S6, S7&S8). Rainfall and incoming shortwave radiation (direct+scattered) from the SAFRAN reanalysis were aggregated at a daily time resolution. The soil temperature values (temperature in the first centimetre of the soil column, variable TG1 in S2M datasets) were computed by the ISBA-Crocus model fed by meteorological information from SAFRAN.

Growing degree days correspond to daily average soil temperature sums (using data for the first centimetre of the soil column) above 0°C and were calculated based on the assumption that plant growth is more affected by cumulated heat than by mean temperature (Körner & Hiltbrunner, 2018). To capture frost intensity and length of frost episodes, FDD was calculated analogously to GDD (daily average ground temperature sums below 0°C) following Choler (2018). GDD was calculated over the growing season, the onset of which was defined by four consecutive days without snow and a soil temperature of at least 4°C in the simulations, and the offset of which was defined by the first day of the winter season with snow on at least four consecutive days. FDD was calculated over the whole year. Both variables were calculated on an annual timescale and then averaged over the whole time period (1988-2018). We logged absolute values of yearly averaged FDD. We calculated the climatic variables over a 30 year time period. This was done as a compromise since plant communities in alpine systems are known to respond to medium-term climatic conditions rather than annual variations (Körner, 2003). Soil communities might instead be more affected by shorter climatic conditions but it has been suggested that soil communities might actually be very tolerant to climatic variations (Thakur & Geisen, 2019; Thakur, 2020; Thakur *et al.* 2020).

To quantify water stress and severity of summer drought, we used an approximation of climate water deficit (CWD). CWD is the difference between potential evapotranspiration and water availability in the soil (Stephenson 1998) and usually accounts for actual evapotranspiration and local soil conditions. Since local soil conditions, and especially available water capacities, are poorly understood in the Alps, we approximated CWD by calculating climate water stress (CWS): daily CWS corresponds to the difference of daily potential evapotranspiration (calculated after Vannier & Braud (2012) using the Penman-Monteith Equation (Allen, Pereira, Raes & Smith, 1998)) and daily precipitation. Water stress increases as values of CWS increase. In the case of precipitation exceeding evapotranspiration there is no water limitation in the soil compartment, therefore CWS values were set to zero (see e.g. Aragão *et al.* 2007). We calculated CWS sums over the growing season for each year between 1988 and 2018, and then averaged these sums to characterize mean water stress and severity of summer drought of the soil compartment.

We calculated cumulative solar radiations over the growing season, and then averaged the cumulative values over the whole period 1988 - 2018.

The graphical lasso

Given that plant-soil linkages are by definition bi-directional and some of the potential relationships between variables are not clearly identified, we used Graphical Lasso (glasso, Friedman, Hastie & Tibshirani, 2007; Mazumder & Hastie, 2012). Glasso is a type of model that is able to decipher the partial correlations between all the variables across our 41 plots without imposing a directional structure, like it would be the case with a structural equation model. In glasso, the partial correlations between all variables are inferred from the inverse of the variance-covariance matrix. Similarly to the lasso regression (Least Absolute Shrinkage and Selection Operator, Tibshirani, 1996), glasso uses a regularization penalty to set all spurious partial correlations to zero. To do so, partial networks are estimated for different values of λ (the penalty coefficient). We used the Extended Bayesian Information Criterion to select the optimal λ , as implemented in the package qgraph (Epskamp, Cramer, Waldorp, Schmittmann & Borsboom, 2012; see also Ohlmann *et al.*, 2018). The obtained regularized partial correlation network was then visualised using Gephi (Bastian, Heymann & Jacomy, 2009). The network consisted of nodes representing the variables and edges which connect the nodes. Two variables were connected if they were conditionally dependent on each other, i.e. they were partially correlated given all other variables in the graph. Reciprocally, two unconnected variables are said to be conditionally independent (i.e. they cannot causally influence each other, Murphy, 2012). Within the glasso, we included several variables representing the different compartments implicated in plant-soil linkages: Plant community, belowground microbial community, physicochemical soil properties and climatic conditions (Fig. 1; Table 1). To assess the importance of a variable within its own group and its importance for other groups, we extracted the degree of each variable (i.e. number of edges that are incident to a given node). We calculated two different measures: the probability of a node to form a connection within its own group (number of realised edges within group/number of possible edges within group), and the probability of a node to form an edge with a node not belonging to its own group (number of realised edges across groups/number of possible edges across groups).

Moreover, we analysed the weights of the edges to estimate the strength of a node (i.e. how important a variable was to the overall plant-soil linkages). The weight of the edges incident to a node corresponds to the strength of its partial correlations. We calculated the sum of absolute partial correlations incident to a node within its own group and the sum of absolute partial correlations incident to a node across groups. The sum of all absolute partial correlations of a node was divided by the number of realised edges to calculate the mean strength of partial correlations.

To assess the importance of interactions between groups, we aggregated the results at the group level, i.e. the probability to form connections as well as the mean partial correlations were calculated for all variables of one group (plant community, EEA, abiotic soil and climate) towards all variables of another group.

Variable selection

From the initial pool of variables (Table 1), a pre-selection was made to avoid redundant information. To choose the most relevant variables, principal component analyses (PCAs) were carried out on plant traits and on climatic variables, respectively. This way, we eliminated MAT, MAP, SR, plant height and leaf C/N from the set of variables.

The glasso was run two times. First, all variables in Table 1 except those eliminated in the PCA step were included (Fig. S4). Then, nodes were excluded that were deemed of minor importance because they were completely unconnected or only connected to other variables in their own group. The network presented in this paper is the result of this process, and only includes five plant community variables (the CWMs LDMC, LMA, RD, LNC, and the canopy variable NDVI_{int}), three abiotic soil variables (C/N, SOM, pH), two climatic variables (GDD, CWS) and two EEA variables (total EEA, vector angle (P/N)). To test the robustness of the result, we ran a regression between the partial correlations from the network containing all variables and the network containing the selection of variables (Fig. S5).

RESULTS

General linkages between biotic plant-soil components and abiotic factors

The probability to observe linkages (Fig. 3a) between the plant community and abiotic components was twice as high for climate as for soil (0.40 and 0.20, respectively). The same pattern was observed for the mean strength of those links (0.44 and 0.26, respectively, Fig. 3b). Enzymatic activity of the soil microbial community was strongly linked to abiotic soil variables (probability 0.67 and mean strength 0.42), but not to climate. There was neither a direct connection between climate and soil properties, nor between the plant community and the soil microbial community (Fig. 3).

Role of the different facets of the plant community in plant-soil linkages

Neither CWMs nor functional diversity indices were linked to microbial activities (Fig. 4, Fig. S4). However, functional diversity measures were completely isolated (spnm, FDiv, FRices and FEve, Fig. S4) and thus removed from the final graph, whereas CWMs of several traits showed clear and strong links to the soil C/N ratio which was a focal variable linking the plant and microbial communities. We observed a partial correlation between RD and soil C/N of -0.24 and of 0.26 between LMA and soil C/N (Fig. 4). NDVI_{int} and soil C/N were positively correlated (0.27).

Variables linked to soil enzymatic activities

We observed no direct linkages between plant traits and ratios of enzymatic activities. However, soil C/N was a focal variable linking plant traits to microbial activity, suggesting that the interaction between plant traits and enzymatic activities passes by litter quality. Soil C/N showed the highest probability to form edges across groups overall (0.44), albeit of mediocre strength (0.29, Table 2). Soil C/N showed a strong linkage to the conservative-exploitative plant continuum. Low soil C/N was associated with low LMA, which in turn was linked to high LNC, which was linked to low LDMC, thus representing a trait assemblage of an exploitative strategy with high investment in photosynthetic leaf area. This spectrum of conservative-exploitative species was indirectly related to soil enzymatic activities via soil C/N. Conservative species (high LMA) and high soil C/N were associated with a high vector angle, indicating that sites with conservative species were less nitrogen and more phosphorus limited than sites with more exploitative species. Conservative species (high LDMC) were also associated with higher water stress (CWS, 0.21).

In addition to plant functional traits, primary productivity played an important role since NDVI_{int} was the link between climate variables and soil C/N. It was positively correlated to GDD (0.7) and negatively to CWS (-0.58), indicating that higher temperatures increased biomass production but associated water stress limited it. NDVI_{int} and soil C/N were positively correlated (0.27) suggesting an increased soil C/N in productive sites.

Soil abiotic characteristics were strongly linked to variables of enzymatic activities. SOM and total EEA showed a strong positive correlation indicating high enzymatic activity in organic matter rich sites, and pH was negatively correlated to both vector angle and total EEA (-0.31 and -0.38, respectively). This suggests strong phosphorus limitation and increased enzymatic activity in acidic soils. Vector length was not related to any other variables (Fig. S4), suggesting that P vs. N limitation is of more importance than carbon vs. nutrient limitation in alpine open habitats.

DISCUSSION

Plant soil linkages and environmental gradients

Studying for the first time the spatial interdependencies between plant functional composition and soil microbial enzymatic activities across grasslands in the French Alps, we found that plant functional composition was mostly associated with climatic variables, while microbial enzymatic activities were primarily related to soil properties. Abiotic factors thus dominate direct biotic linkages in our study system which confirms what has been proposed before: that abiotic factors are of primary importance in mountain systems (Neuwinger, 1970; Körner, 2003). Our results further revealed that an interdependency between plant traits and soil C/N links the aboveground community to the belowground community. This is congruent with the hypothesis that plant traits play a central role in plant-soil linkages through control of litter quality (Schweitzer *et al.*, 2008; Lau & Lennon, 2011; van der Putten *et al.*, 2013). Moreover, our results showed that in alpine open habitats effects of climate propagate to the soil community through plant traits. This is in concordance with previous studies that demonstrated links between climate and plant traits (Mayor *et al.*, 2017), as well as indirect effects of climate on the soil community via plant traits (Delgado-Baquerizo *et al.*, 2018).

However, in contrast to previous studies (de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2018), we neither found a direct link between soil microbial community activity and plant functional CWMs, nor between soil microbial community activity and climatic variables. This might be due to the fact that the focus of our study was assessing the functioning of the microbial community through extracellular enzymatic activity (e.g. recycling of organic matter) rather than the composition of the microbial community itself. The link between microbial community composition and function is not necessarily straightforward. Potential changes in microbial community composition, resulting from changes in plant functional traits for example, that could occur here might not have had an impact if there is some level of functional redundancy in the microbial community for the extracellular enzymatic activities we measured (Louca *et al.*, 2018). Future studies considering diversity or composition of microbial communities along with their function could reveal more direct links with plant traits as observed in de Vries *et al.* (2012) and Delgado-Baquerizo *et al.* (2018), and help understand spatial interdependencies between below- and aboveground communities along large environmental gradients. An explanation for the missing link between soil microbial and climatic variables may be the 30-year time period over which the climatic variables were calculated. This period was chosen because plant communities in alpine systems are known to respond to medium-term climatic conditions rather than annual variations (Körner, 2003). While soil communities might instead be more affected by shorter climatic conditions it has also been suggested that soil communities might actually be very tolerant to climatic variations (Thakur & Geisen, 2019; Thakur, 2020; Thakur *et al.* 2020). The choice of the time period over which climatic variables are calculated is, in a large-scale ecosystem study, necessarily a compromise between the studied compartments (see also last section of the discussion).

Role of the different facets of the plant community in plant-soil linkages

Contrasting the mass-ratio-hypothesis (Grime, 1998) with the diversity-function-hypothesis (Tilman *et al.*, 1997; Hooper *et al.*, 2005), we found that CWMs of plant traits were more important than diversity metrics, supporting the mass-ratio-hypothesis. CWMs showed clear and strong linkages to soil C/N, propagating on to microbial activities and SOM content, indicating a strong effect on organic matter decomposition and the recycling of nutrients (Garnier *et al.*, 2004; Queded *et al.*, 2007; Fortunel *et al.*, 2009; Grigulis *et al.*, 2013; Lavorel, 2013). These results are consistent with the growing body of evidence for the mass-ratio-hypothesis as a central mechanism controlling ecosystem functioning and services (Lavorel, 2013; Li *et al.*, 2017). They also confirm that it is the linking mechanism between plants and the functional properties of microbial communities (Grigulis *et al.*, 2013; Piton, Legay, *et al.*, 2020).

The isolation of functional diversity indices in our analyses may be in part due to the mountain context of our study. Hooper *et al.* (2005) suggested that ecosystems might be less defined by functional diversity in challenging abiotic conditions. They also argued that species with different response traits to environmental changes are needed under increasing temporal and spatial variability in order to ensure a stable supply of ecosystem functions. Furthermore, it has been shown that mass ratio effects better explain individual functions, but that multifunctionality of ecosystems is more driven by diversity effects (Le Bagousse-Pinguet *et al.*, 2019). Therefore, considering today's climate and land-use changes and biological invasions, even a system where the diversity-function-hypothesis does not play an important role under current conditions may depend on trait diversity if certain thresholds are crossed in the future. Thus, although our results confirm the importance of CWMs for ecosystem functioning (e.g. decomposition and nutrient recycling) their importance for ecosystem stability still needs further exploration (e.g. Piton, Legay, *et al.*, 2020), especially in alpine systems where species' trait values may vary a lot depending on altitude due to high plasticity (Albert, Thuiller, Yoccoz, Douzet, *et al.*, 2010; Albert, Thuiller, Yoccoz, Soudan, *et al.*, 2010).

Variables linked to soil enzymatic activities

It is well understood that plant traits are linked to microbial community composition and functioning, directly and via plant litter quality (Grigulis *et al.*, 2013; Fanin *et al.*, 2014; Legay *et al.*, 2014; Martinez-Almoyna *et al.*, 2020). In our study, plant traits associated with the plant conservative-exploitative continuum (LMA, LNC and LDMC) were indirectly connected to SOM, as well as soil enzymatic activities, via a central link between plant traits and soil C/N. This supports at biogeographic scale the hypothesis that litter quality rather than quantity plays a central role in microbial functions involved in aboveground-belowground linkages in grassland ecosystems, as has been shown previously also for soil microbial community composition and diversity in studies of temperate grasslands in England and Germany (de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2018).

Interestingly, our partial correlation network is consistent with the expected ecosystem functioning along a conservative-exploitative continuum (Moore, 1988; Bardgett & Wardle, 2010; Mulder *et al.*, 2013). On the conservative side, reduced organic matter quality (high soil C/N) associated with conservative plant traits favours SOM accumulation, increasing total enzymatic activity. High soil

C/N was also associated with an increased investment of microbial communities in P-acquisition relative to N-acquisition, suggesting that conservative plant traits and high soil C/N are also associated with a high N/P ratio of resources available for microbes. The link between soil C/N and microbial nutrient acquisition strategies might be central in the feedback from soil to plants. In infertile soils, microbial communities immobilize nutrients in their biomass, releasing less nutrients to the soil (Mooshammer *et al.*, 2014; Zechmeister-Boltenstern *et al.*, 2015). This creates a negative feedback-loop since a nutrient poor soil will result in a more conservative plant community which will then produce more recalcitrant litter increasing further SOM accumulation and the nutrient limitation of microbial communities (Wardle *et al.*, 2004; de Vries & Bargett, 2012).

Our network also showed soil C/N to be linked with plant community productivity (NDVI_{int}) and root depth. High plant productivity was associated with a warm growing season, low water deficit and exploitative plant traits (low LMA). It was also positively associated with soil C/N, likely explained by higher plant derived C input in the soil with higher productivity. On the contrary, high root depth associated with high water deficit (stress resistance strategy) decreased soil C/N, possibly because a higher fraction of the plant derived C was released deeper into the soil and thus could not be captured in our soil data from the upper horizon. Our results also suggest stronger microbial phosphorus than nitrogen limitation (high vector angle) and increased enzymatic activity in acidic soils, in accordance with Piton, Legay, *et al.* (2020). In acidic soils (mean pH of our sites was 5.5), leaching of acids towards the bedrock releases (Fe, Al or Mn) cations. These cations form compounds with bioavailable forms of phosphorus, such as H₂PO₄⁻, and hence decrease P availability (Wild, 1950; Iqbal, 2012).

Critical aspects and perspectives

Our study gives insights about linkages between plant and microbial soil communities in alpine habitats at large scales, and we show how abiotic climatic conditions and soil properties influence these linkages. However, our study is not without flaws. First, there may be a conflict of scales in our analysis. Plant and microbial soil communities have a very different temporal turnover, i.e. composition and abundances may change faster in microbial than in plant communities, and microbial communities may hence respond faster to changes in environmental conditions (Bardgett and Wardle, 2010; but see Thakur & Geisen, 2019; Thakur, 2020; Thakur *et al.* 2020). They may thus be more determined by short-term fluctuations in abiotic conditions while plant communities may respond more to long-term changes. This may create a mismatch in temporal scales when analyzing both components at the same time. For example, we calculated climatic variables like growing degree days (GDD) over a period that could be considered more of a determinant of the plant community. To determine whether this temporal mismatch was truly an issue, we compared GDD calculated over a 30 years' time period (as used here), with the GDD calculated over 10 years and over the year before sampling for all our 41 plots. All correlations were very high, demonstrating that the differences between plots remain relatively constant whatever the time-scale used to calculate growing degree days (Fig. S7, S8). We are thus confident that this should not influence the results and the conclusion of our paper. In addition to a temporal mismatch, there may also be a spatial one. The quantitative prediction of precipitation in mountainous areas can be biased because precipitation is a very local phenomenon that changes from one mountain massif to another (Roe, 2005; Quintana-Segui *et al.*, 2008; Quintana-Segui *et al.*, 2017). Spatial variability

in precipitation may therefore be difficult to capture with climate models if few observation stations are available (Hofstra, New & McSweeney, 2010). However, while SAFRAN is known to overestimate the number of precipitation days and underestimate high precipitation events (Quintana-Segui, Turco, Herrera & Miguez-Macho, 2017), it is very likely that plot differences (i.e. the ranking between the plots) are relatively robust to these uncertainties and should thus not influence the Graphical lasso estimation.

Second, plant-soil linkages are complex and they may be affected by factors that we did not include in this study, such as herbivores and soil meso- and macrofauna. Furthermore, we did not include direct measures of diversity or composition of the microbial community but only variables related to their activities. Specifically, we did not use environmental DNA metabarcoding approaches because they do not provide reliable information on the biomass of different organisms (Taberlet, Bonin, Zinger & Coissac, 2018; Calderón-Sanou, Münkemüller, Boyer, Zinger & Thuiller, 2020). It would thus neither have been possible to calculate ratios of fungal and bacterial biomass, nor would we have had information about abundances of oligotrophic and copiotrophic groups. While we showed that functional diversity of the plant community did not play a role in our study system, we cannot exclude the possibility that diversity of the microbial community did. In addition, we showed in our study that litter quality may be a key determinant of microbial functions in alpine grassland ecosystems. We deduced this from measures of topsoil C/N content which we interpreted as a proxy of litter quality. In future studies it may hence be of interest to include direct measures of litter quality.

Third, it is important to note that we quantified EEA *in vitro* and therefore used measures of potential enzymatic activity and not *in situ* activity. It has been argued that *in vitro* assays may be a limited proxy for EEA in real conditions since substrate diffusion and abundance, as well as soil type and temperature are not reflected in *in vitro* assays (Wallenstein and Weintraub, 2008; Bell *et al.*, 2013). However, *in situ* measurements provide only a snapshot of the belowground community's activity and may therefore not adequately represent longer-term linkages between the plant and the soil microbial communities.

Last, we chose to study plant-soil-linkages with the graphical lasso because it is difficult or even impossible to uncover interactions through experiments at large scales. More importantly, we do not know if observed patterns result from the plant community influencing the soil community, or the other way around, or both influencing each other reciprocally. Hence, an undirected partial correlations network is a very well-suited method to disentangle direct and indirect effects between the plant and the soil microbial communities, and to look at biogeographic patterns. Nevertheless, experimental validation is necessary to determine causal pathways, which is especially important considering the potential effects of rising temperatures or changes in precipitation on plant-soil relationships.

Conclusion

Studying the spatial interdependencies between the plant functional composition, soil microbial enzymatic activities and abiotic conditions across the French Alps, we found abiotic drivers to be key elements. Plant traits were more strongly controlled by climate, whereas enzymatic activities were more associated with soil abiotic properties. The connections between climate and soil biotic and abiotic properties were only indirect through plant trait association with soil C/N. At the same time, the links between microbial enzymatic activities and plant traits through soil C/N highlighted the role of plant-soil interdependencies in ecosystem responses to abiotic changes. The observed plant-soil linkages are well in concordance with the conservative-exploitative continuum with soil C/N as an important player. Our study is one of the first identifying a signal of the conservative-exploitative plant continuum and microbial nutrient acquisition strategies in patterns of co-distributions of plant functional traits and microbial activity on a biogeographic scale (the French Alps) in alpine ecosystems. It thus demonstrates how the soil functioning can be integrated in studies of ecosystem shifts under environmental change at large spatial scales.

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Statement of Significance

The tight links between plant and soil communities are major drivers of biodiversity responses to environmental change. However, we ignore how those links vary over biogeographic scales. Here, we used partial correlation networks to investigate plant-soil linkages along fourteen elevational gradients in the French Alps. We found tight linkages of plant traits with microbial activities, the former being driven by climate and the latter by soil properties. Climate did not affect soil properties directly, but through plant functional traits. Overall, we demonstrate how soil functioning can be integrated in studies of ecosystem shifts under environmental change at large spatial scales.

Authors contributions

WT and TM conceived the ideas, field observations and lab measurements were carried out by the ORCHAMP consortium. WT, CMA and AS collected soil samples, GP, AS and AF analysed the enzymatic activities and LB performed the trait measurements. JR managed and maintained databases of traits, climatic variables and ORCHAMP field measurements, PC provided NDVI data, CMA calculated the climatic indices. SSW performed the modelling work and all subsequent analyses. GP, AF and JP gave additional perspectives to the paper. SSW wrote the first draft of the manuscript and all authors contributed substantially to revisions and gave final approval for publication.

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Tables

Table 1: Overview of variable pool from which a selection was made to use in the graphical lasso.

Variable	Acronym	Unit	Data source	Mean (median) \pm st. deviation	[min, max]	Transformation
Extracellular enzymatic activity						
Total EEA	Total EEA	nmol/(h *g dry)	Orchamp	12677 (12174) \pm 6520	[3713, 29858]	ln
Vector length (proportion)	EEC/EEN	°	Orchamp	0.79 (0.78) \pm 0.08	[0.63, 1.00]	-
Vector angle (proportion P/N)	EEN/EEP	-	Orchamp	66.1 (65.7) \pm 6.0	[53.5, 79.1]	-
Physico-chemical soil properties						
Soil organic matter	SOM	%	Orchamp	25.1 (23.3) \pm 1.4	[8.5, 55.2]	log10
Carbon to nitrogen ratio	Soil C/N	-	Orchamp	14.68 (14.42) \pm 0.12	[10.96, 18.41]	log10
pH	pH	-	Orchamp	5.45 (5.43) \pm 0.02	[4.01, 7.38]	-
Vegetation variables						
Leaf nitrogen content (CWM)	LNC	mg/g		21.4 (20.9) \pm 3.3	[13.6, 31.0]	ln
Leaf carbon to nitrogen ratio (CWM)	C/N	-		22.8 (22.4) \pm 4.1	[14.8, 38.2]	log10
Leaf dry mass per area (CWM)	LMA	mg/mm ²		0.068 (0.067) \pm 0.014	[0.033, 0.098]	log10
Leaf dry matter content (CWM)	LDMC	mg/g		296 (291) \pm 41	[198, 400]	sqrt
Plant height (CWM)		cm		26 (25) \pm 11	[10, 59]	ln
Root depth (CWM)	RD	-	Landolt <i>et al.</i> 2010	2.02 (2.00) \pm 0.02	[1.24, 3.04]	log10
Species richness	spnm	Numbe	Orchamp	55 (55) \pm 13	[32, 82]	-
Standard effect size of functional richness	FRic _{ses}	-		-0.08 (-0.08) \pm 0.04	[-0.15, -0.03]	-
Functional evenness	FEve	-		0.57 (0.57) \pm 0.07	[0.40, 0.70]	-
Functional divergence	FDiv	-		0.94 (0.95) \pm 0.01	[0.87, 0.98]	-
Integrated normalized difference vegetation index (Proxy for biomass production)	NDVI _{int}	-	Terra MODIS 2000-2018	80 (86) \pm 38	[7, 158]	-
Climatic variables						
Mean annual temperature	MAT	°C	Safran-Crocus 1988-2018	3.10 (2.97) \pm 0.77	[1.75, 5.05]	-
Mean total annual precipitation	MAP	mm/ye ar	Safran-Crocus 1988-2018	673 (650) \pm 223	[308, 1094]	-
Growing degree days (growing season)	GDD	°C/year	Safran-Crocus 1988-2018	1164 (1087) \pm 289	[660, 1881]	-
Freezing degree days (whole year)	FDD	°C/year	Safran-Crocus 1988-2018	42 (38) \pm 21	[16, 98]	ln on absolute
Mean climate water stress (growing season)	CWS	mm/ye ar	Safran-Crocus 1988-2018	276 (263) \pm 46	[179, 369]	-
Mean solar radiation (growing season)	SR	kJ/(m ² * year)	Safran-Crocus 1988-2018	282823 (280069) \pm 27554	[202322, 367770]	-

Table 2: Degree analysis of the partial correlations network presented in Fig. 4. "Edges within" corresponds to the probability to observe partial correlations between a given variable and other variables that belong to its own group. "Mean strength within" corresponds to the mean sum of all absolute partial correlations that are realised within the group. "Edges across" and "Mean strength across" are analogous metrics to the ones cited before concerning partial correlations across groups. Abbreviations: LNC: leaf nitrogen content, RD: root depth, LMA: leaf mass per area, LDMC: leaf dry matter content, NDVI_{int}: integrated normalized difference vegetation index, soil C/N: soil carbon to nitrogen ratio, SOM: soil organic matter content, GDD: growing degree days, CWS: climate water deficit, total EEA: total enzymatic activity.

Variable	Group	Edges within	Mean strength within	Edges across	Mean strength across
LNC	Vegetation	0.50	0.49	0	0
RD	Vegetation	0.25	0.22	0.29	0.26
LMA	Vegetation	0.50	0.38	0.14	0.26
LDMC	Vegetation	0.25	0.50	0.14	0.21
NDVI _{int}	Vegetation	0.50	0.25	0.43	0.52
soil C/N	Soil	0.50	0.23	0.44	0.29
SOM	Soil	0.50	0.23	0.11	0.57
pH	Soil	0	0	0.22	0.35
GDD	Climate	1	0.81	0.10	0.70
CWS	Climate	1	0.81	0.30	0.36
Vector angle (proportion P/N)	Enzymatic activity	0.00	0.00	0.20	0.36
Total EEA	Enzymatic activity	0.00	0.00	0.20	0.48

Figure captions

Figure 1 | Linkages between aboveground plant communities and belowground microbial communities and abiotic factors affecting them. Variables defining the compartments plant community, soil properties and climate are written next to them: LNC – leaf nitrogen content, LDMC – leaf dry matter content, LMA – leaf mass per area, SOM – organic matter, C/N – soil carbon nitrogen ratio. References for the specific linkages are indicated by numbers: 1: Bowman *et al.*, 2004; 2: de Vries *et al.*, 2012; 3: Freppaz *et al.*, 2007; 4: Grigulis *et al.*, 2013; 5: Legay *et al.*, 2014; 6: Martinez-Almoyna *et al.*, 2020; 7: Mayor *et al.*, 2017; 8: Piton, Legay, *et al.*, 2020; 9: Quedsted *et al.*, 2007; 10: Sundqvist, Sanders & Wardle, 2013, and references therein; 11: van der Putten *et al.*, 2016, and references therein; 12: Wardle *et al.*, 2004, and references therein.

Figure 2 | The ORCHAMP observatory network in the French Alps (with years of sampling) and measurements that were taken on the plots of the individual elevational gradients.

Figure 3 | Probability of observing links between compartments (a) and mean strength of links between compartments (b).

Figure 4 | Graph of a partial correlations network in alpine communities, including plant community weighted means, soil microbial enzymatic activities, climatic variables and physico-chemical soil properties. Positive partial correlations are represented by dotted edges, negative ones by continuous ones. The weight of the edges (thickness) corresponds to the absolute strength of their partial correlations. Abbreviations: RD: root depth, LMA: leaf mass per area, LNC: leaf nitrogen content, LDMC: leaf dry matter content, NDVI_{int}: integrated normalized difference vegetation index, GDD: growing degree days, CWS: climate water deficit, soil C/N: soil carbon to nitrogen ratio, SOM: soil organic matter content, total EEA: total enzymatic activity.

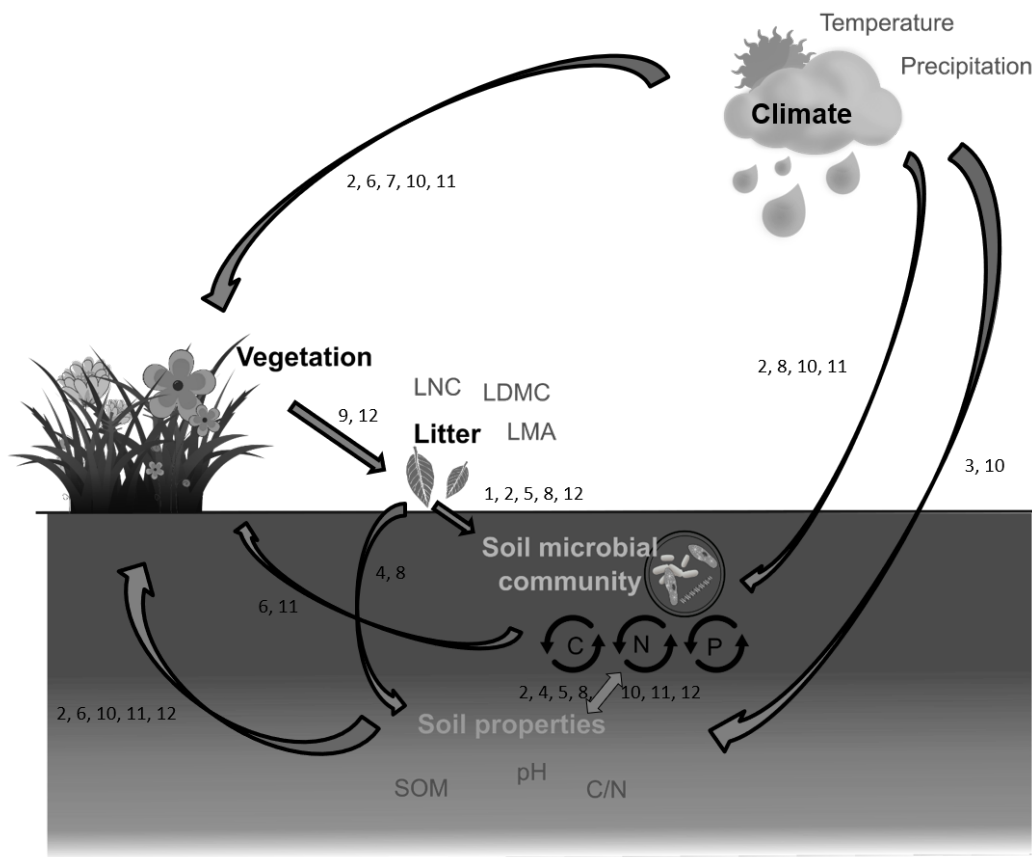


Figure 1

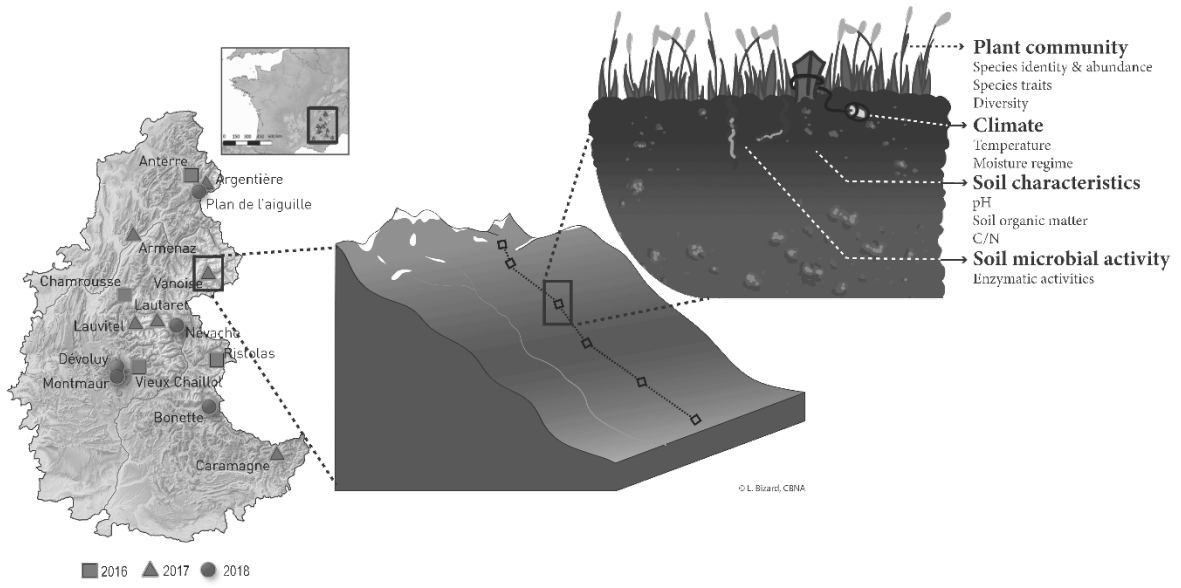


Figure 2

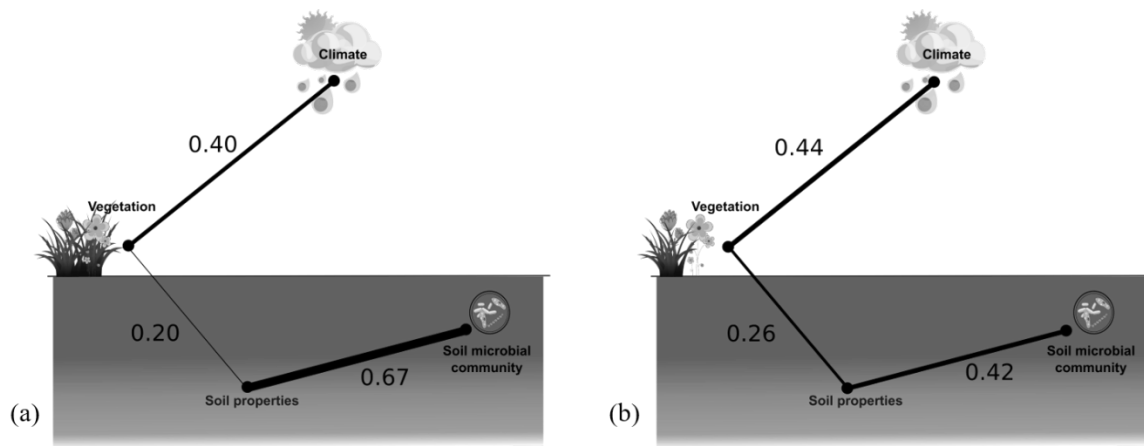


Figure 3

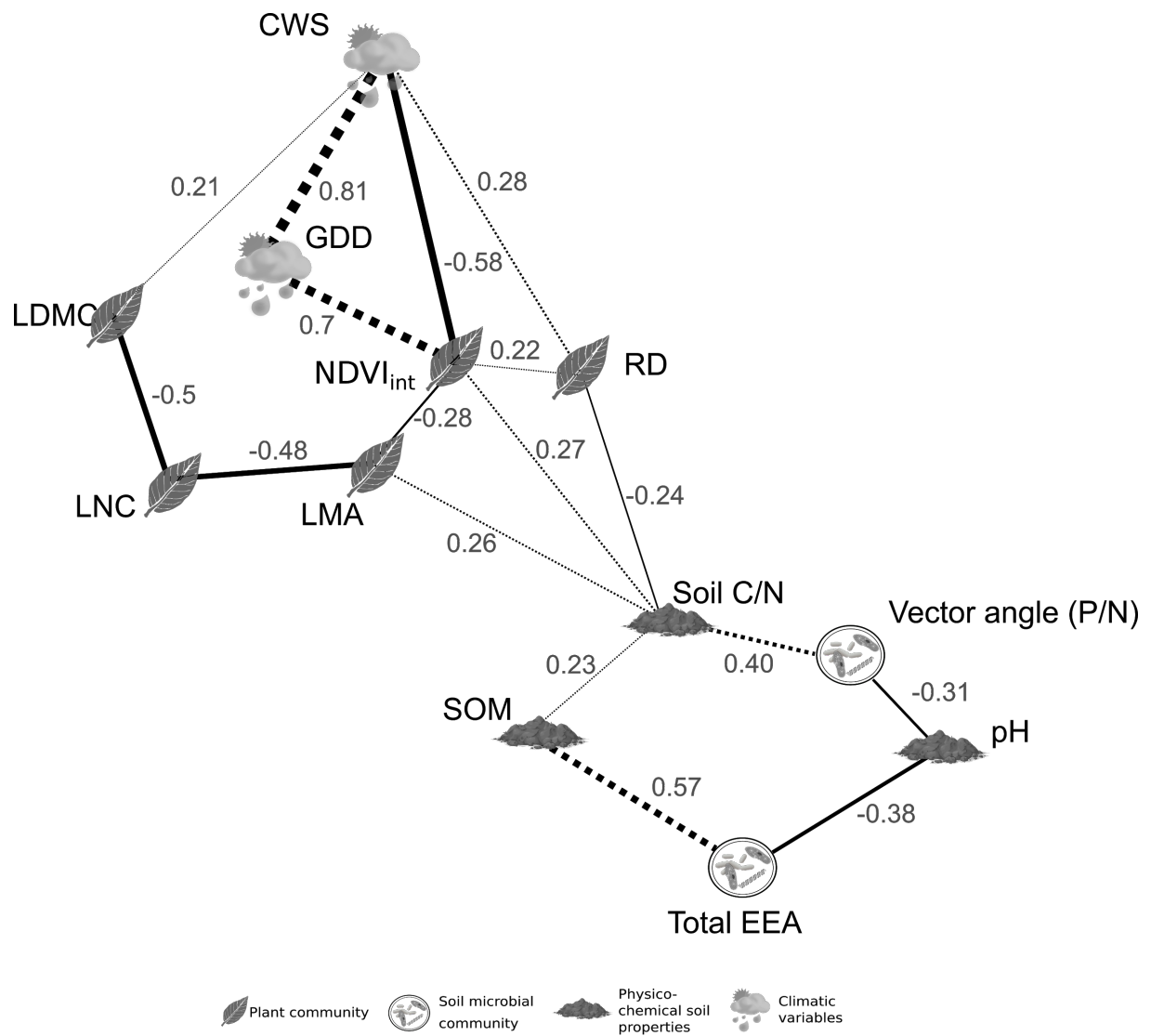


Figure 4

Discussion générale



Échantillonnage de la faune épigée, session ORCHAMP 2018

Dans un contexte où les activités humaines modifient l'environnement (ex. changement climatique, érosion des sols) et poussent la Terre vers une sixième extinction de masse (Barnosky *et al.*, 2012, 2011), il semble urgent de prédire à quoi ressembleront les écosystèmes du futur. Une des possibilités pour atteindre cet objectif consiste à modéliser le fonctionnement des écosystèmes dans l'espace géographique. Cependant, certains obstacles subsistent et empêchent de prédire et cartographier le fonctionnement des écosystèmes à large échelle. Mon travail de thèse s'attachait à améliorer trois points en particulier : 1/ la prise en compte la variabilité spatiale des conditions environnementales, notamment du climat et du sol, 2/ l'intégration des interactions entre espèces de plantes et du sol, notamment les interactions trophiques, 3/ la modélisation du fonctionnement de l'écosystème dans son ensemble, à l'aide de fonctions mesurées à l'échelle de l'écosystème et de façon spatialement explicite

Dans cette dernière partie, pour chacun de ces trois points, je fais la synthèse des avancées réalisées, des lacunes de mon travail, et des perspectives d'amélioration.

I. Synthèse du travail effectué pour la prise en compte de la variabilité spatiale des conditions environnementales dans la modélisation du lien environnement – biodiversité – fonctionnement des écosystèmes.

Dans un premier temps (CHAPITRE 1), nous nous sommes placés le long d'un seul gradient d'altitude et avons étudié l'importance relative du climat et des propriétés physico-chimiques du sol sur les communautés de plantes et du sol et le fonctionnement des écosystèmes. Ce premier chapitre a permis de mettre en évidence le rôle clef joué par les propriétés physico-chimiques du sol pour le fonctionnement des écosystèmes. Cependant, de façon plus surprenante, nous n'avons trouvé d'effet significatif du climat ni sur la multifonctionnalité, ni sur aucune des fonctions écosystémiques étudiées séparément. Nous nous sommes demandés si cela pourrait être dû à un effet d'échelle, et si nous pourrions retrouver un effet du climat sur le fonctionnement à l'échelle régionale. Ainsi, dans les trois chapitres qui ont suivi, nous avons changé d'échelle pour nous placer le long de plusieurs gradients d'altitude. Cela nous a permis de différencier les effets de différentes variables climatiques et propriétés physico-chimiques du sol (CHAPITRES 2, 3, 4), puis d'utiliser des méthodes de sélection de variables pour ne garder que les meilleurs prédicteurs environnementaux des communautés de plantes (CHAPITRE 3) et du fonctionnement des systèmes plantes-sol (CHAPITRE 4).

En ce qui concerne le premier point - l'environnement - mes travaux de thèse confirment qu'il est essentiel de prendre en compte des variations spatiales des conditions environnementales pour prédire correctement le fonctionnement des écosystèmes. En premier lieu, nous avons démontré de façon récurrente que les propriétés physico-chimiques du sol jouent un rôle direct clef pour prédire le fonctionnement des écosystèmes (CHAPITRES 1, 2, 4), tandis que l'influence du climat semblait être surtout importante à large échelle, et plus indirecte (CHAPITRES 2,4). Si

jusqu'il y a quelques années, beaucoup d'études du fonctionnement des écosystèmes ignoraient la variabilité des conditions environnementales (Adhikari & Hartemink, 2016; Brose & Hillebrand, 2016), ou ne différençiaient pas l'effet du climat et de celui du sol (ex. Soliveres *et al.*, 2016), ce résultat est maintenant bien documenté. En parallèle de ma thèse, de plus en plus de publications ont également confirmé l'effet direct et prépondérant des propriétés physico-chimiques du sol sur les fonctions écosystémiques, en particulier les fonctions liées au sol (ex. cycles des nutriments, décomposition, Legay *et al.*, 2016; Manning *et al.*, 2015; Qiu, Xie, Xu, & Pott, 2018; Van Eekeren *et al.*, 2010) et la multifonctionnalité (Le Bagousse-Pinguet *et al.*, 2019; Liu, Shi, & Zhang, 2021; Nazaries *et al.*, 2021). En outre, les résultats de Crowther *et al.* (2015), Delgado-Baquerizo *et al.* (2017, 2016), et Buzzard *et al.* (2019) semblent aussi montrer que même à très large échelle, l'influence du climat sur le fonctionnement des écosystèmes pourrait être modulée par certaines propriétés du sol.

En second lieu, il a été intéressant de constater que différents prédictors environnementaux expliquent la structure de chaque groupe trophique (CHAPITRES 1, 2, 3). Ainsi, les effets indirects de l'environnement sur le fonctionnement varient selon quelle association *prédictor environnemental - groupe trophique* est considérée. Cela suggère que les effets indirects de l'environnement peuvent se compenser (CHAPITRE 2). Cependant, on sait finalement très peu de choses de ces effets indirects de l'environnement, via la communauté de plantes et du sol, sur le fonctionnement des écosystèmes. Tout d'abord, cela est dû au fait que les prédictors environnementaux de la structure de la communauté des plantes et du sol sont mal connus (Chu, Gui-Feng, Ma, Fan, & Delgado-Baquerizo, 2020). En ce qui concerne les plantes, pourtant au cœur des études de biogéographie depuis plusieurs siècles (von Humboldt, 1805), on commence tout juste à intégrer des propriétés édaphiques dans les modèles de distributions d'espèces (CHAPITRE 3, Buri *et al.*, 2017, 2020; Dubuis *et al.*, 2013). De plus, il y a très peu d'études sur la biogéographie des organismes du sol (mais voir les études à l'échelle globale de Bates *et al.*, 2013, pour les protistes; Fierer & Jackson, 2006, pour les bactéries; Song *et al.*, 2017, pour les nématodes; Tedersoo *et al.*, 2014 pour les champignons), beaucoup ne concernent qu'une ou peu d'espèces, et elles donnent peu d'informations sur les prédictors environnementaux qui structurent la composition des différents groupes trophiques (ex. Fiera & Ulrich, 2012; Schatz, 2004). Enfin, bien que le nombre de publications qui lient la biodiversité multi-trophique aux fonctions écosystémiques augmente depuis une dizaine d'années, celles qui mettent l'accent sur les changements de composition restent rares (mais voir Mori, Isbell, & Seidl, 2018; Xiong *et al.*, 2021; Yan, Zhang, Buyantuev, Liu, & Niu, 2020). Par conséquent, ces deux lacunes combinées limitent encore notre capacité à quantifier les effets indirects de l'environnement sur le fonctionnement des écosystèmes, et à identifier les cas où ces effets indirects peuvent se compenser.

II. Synthèse du travail effectué pour l'intégration des interactions entre espèces dans la modélisation du lien environnement – biodiversité – fonctionnement des écosystèmes.

Nous avons commencé par intégrer les interactions entre espèces à l'aide d'une approche multi-trophique des communautés (CHAPITRES 1 et 2). Dans un premier temps (CHAPITRE 1), nous avons utilisé des groupes trophiques peu résolus sans intégrer les interactions trophiques entre ces groupes de manière explicite. Malgré cela, les changements de composition de certains groupes clés (les champignons saprophytes) se sont révélés être des prédicteurs directs du fonctionnement des écosystèmes, en particulier de la productivité et de la multifonctionnalité (CHAPITRE 1). De plus, ce chapitre soulignait que les changements de composition des autres groupes trophiques influencent aussi indirectement le fonctionnement des écosystèmes, via leurs interrelations avec les champignons saprophytes. Ces deux résultats nous ont poussés, dans un second chapitre, à nous intéresser plus particulièrement à la régulation de la décomposition par le réseau du sol. Nous avons donc explicitement intégré les interactions trophiques entre les décomposeurs (bactéries et champignons) et les groupes trophiques qui s'en nourrissent pour tester l'hypothèse de l'existence d'une régulation trophique des microbes et de la fonction de décomposition (CHAPITRE 2). Cependant, cette approche hiérarchique ne permettait pas facilement d'intégrer explicitement les autres types d'interactions entre les groupes trophiques. Le mutualisme indirect entre décomposeurs et plantes, par exemple, influence également les fonctions écosystémiques, comme en témoignent l'importance des champignons saprophytes et l'absence de lien entre plantes et productivité dans le CHAPITRE 1. Dans une seconde partie de cette thèse (CHAPITRES 3 et 4), nous avons donc mis l'accent sur les associations spatiales entre les plantes et les microbes uniquement, afin de faire un premier pas vers la prise en compte de leurs interactions indirectes dans la modélisation spatiale du fonctionnement des écosystèmes. Nous avons changé de perspective et utilisé le cadre conceptuel des traits de réponse et d'effet appliqué aux communautés multi-trophiques. Ainsi, nous avons intégré les interactions indirectes entre plantes et microbes dans la modélisation des distributions des plantes (à l'aide de modèles de distributions multi-espèces, CHAPITRE 3), ainsi que dans la modélisation de la productivité primaire et de l'activité microbienne de décomposition (à l'aide d'une approche non-dirigée, le *graphical lasso*, CHAPITRE 4). Pour cela, nous avons mis en relation des proxys des traits moyens pondérés de la communauté microbienne (considérés comme traits trophiques et d'effet) avec des traits liés à la stratégie d'acquisition des ressources des plantes (considérés comme traits trophiques et de réponse, INTRO., Box 2, Lavorel *et al.*, 2013).

Pour résumer ce qui concerne l'approche multi-trophique des communautés (le deuxième point), mes travaux de thèse confirment que la diversité multi-trophique, notamment la diversité horizontale de certains groupes clés, est aussi importante que l'environnement pour prédire le fonctionnement des écosystèmes dans l'espace géographique (CHAPITRES 1, 2, 4). Ce résultat est également récurrent dans les quelques études multi-trophiques du lien entre biodiversité et fonctionnement des écosystèmes. Les décomposeurs (microbes), les plantes et les herbivores ont régulièrement été identifiés comme étant des groupes trophiques clés pour le fonctionnement des écosystèmes, y compris pour les fonctions qui ne sont pas directement reliées à leur activité

biologique (ex. la nitrification pour les producteurs primaires, Soliveres *et al.*, 2016) et pour la multifonctionnalité (Chen *et al.*, 2020; Lefcheck *et al.*, 2015; Li *et al.*, 2019; Schuldt *et al.*, 2018; Soliveres *et al.*, 2016).

Cependant, au fur et à mesure que ces preuves s'accumulent, il devient difficile de généraliser quels sont les groupes trophiques les plus importants pour le fonctionnement des écosystèmes sans i/ mentionner le lien à l'environnement et au type d'écosystème (ex. le CHAPITRE 2 et Chen *et al.* (2020) montrent que les bactéries sont plus importantes que les champignons dans les habitats ouverts, tandis qu'en forêt, le CHAPITRE 2, Li *et al.* (2019) et Schuldt *et al.* (2018) démontrent un lien avec les fonctions écosystémiques plus fort pour les champignons que pour les bactéries), ii/ considérer les groupes trophiques du sol et les groupes trophiques épigés en même temps (ex. Chen *et al.* (2020) et Delgado-Baquerizo *et al.* (2017) considèrent seulement les microbes, Lefcheck *et al.* (2015) ne prend pas en compte la communauté microbienne, ma thèse ne considère pas les groupes trophiques épigés), iii/ intégrer explicitement les interactions trophiques qui lient les groupes trophiques basaux aux niveaux trophiques plus hauts (Barnes *et al.*, 2014; Duffy *et al.*, 2007; Schuldt *et al.*, 2018). Concernant ce dernier point, en intégrant pour la première fois explicitement des interactions trophiques dans la modélisation du lien environnement – biodiversité – fonctionnement grâce à l'utilisation de modèles d'équations structurelles, ma thèse confirme également que d'autres groupes trophiques peuvent influencer indirectement les fonctions écosystémiques, par exemple via une régulation *top-down* par les interactions trophiques (CHAPITRE 2). Ainsi, nous ouvrons la porte à de meilleures prédictions des fonctions écosystémiques dans l'espace géographique et à large échelle (CHAPITRE 2).

En revanche, nos résultats montrent aussi que les autres types d'interactions non-dirigées, notamment le mutualisme indirect qui lie les plantes aux communautés microbiennes, sont plus difficiles à intégrer explicitement pour prédire le fonctionnement des écosystèmes (CHAPITRES 3 et 4). En effet, ni dans le CHAPITRE 3, ni dans le CHAPITRE 4, nous n'avons décelé un lien direct entre traits moyens pondérés microbiens et traits moyens pondérés des plantes, pourtant liés à leurs stratégies respectives d'acquisition des ressources, et choisis pour bien représenter le mutualisme indirect qui lie les plantes et les microbes (Piton *et al.*, 2020). Si on le compare aux multiples publications récentes qui font état d'associations spatiales à larges échelles entre traits des plantes et propriétés de la communauté microbienne, ce résultat est plutôt surprenant (Boeddinghaus *et al.*, 2019; Buzzard *et al.*, 2019; de Vries *et al.*, 2012; Delgado-Baquerizo *et al.*, 2017; Legay *et al.*, 2014, 2016; Piton *et al.*, 2020; Pommier *et al.*, 2018). Notamment, l'expérience de Piton *et al.* (Piton *et al.*, 2020) montre spécifiquement que les traits moyens pondérés des plantes et des microbes sont significativement associés au sein de systèmes plantes-sols extraits de prairies alpines. Cependant, dans la littérature, l'association entre traits des plantes et propriétés de la communauté microbienne est finalement souvent soit explicitement indirecte, via une médiation des propriétés physico-chimiques du sol (comme dans le CHAPITRE 4, Buzzard *et al.*, 2019; Mayor *et al.*, 2017; Pommier *et al.*, 2018), soit dépendante du contexte (en particulier de la disponibilité en nutriments, Legay *et al.*, 2016). Il semble donc essentiel de prendre en compte les rétroactions entre les groupes trophiques (particulièrement plantes et microbes) et les propriétés physico-chimiques du sol pour intégrer explicitement le mutualisme indirect qui lie les communautés de plantes et de microbes dans les modèles prédictifs du fonctionnement des écosystèmes.

III. Synthèse du travail effectué pour la modélisation du fonctionnement des écosystèmes dans son ensemble

Dans un premier temps (CHAPITRE 1), nous avons modélisé séparément différentes fonctions écosystémiques résumées (liées à la productivité, au cycle de l'azote et au lessivage de l'azote) et une mesure de multifonctionnalité. Les résultats de ce premier chapitre suggèrent que des boucles de rétroaction peuvent exister entre deux fonctions écosystémiques (ex. entre décomposition et productivité), ou entre fonctions et groupes trophiques (ex. entre décomposition et composition de la communauté végétale). Cela nous a conduit (CHAPITRES 3 et 4) à remettre en question la vision hiérarchique du lien environnement-biodiversité-fonctionnement utilisée dans les deux premiers chapitres. Ainsi, dans un CHAPITRE 3, nous testons l'hypothèse selon laquelle la fonction de décomposition pourrait contraindre la composition des communautés de plantes, et dans un CHAPITRE 4, nous cartographions des liens entre la communauté microbienne, sa fonction de décomposition, la communauté de plantes et sa productivité primaire.

En ce qui concerne la modélisation du fonctionnement de l'écosystème dans son ensemble (le troisième point), mes travaux suggèrent que les différentes fonctions ont des prédicteurs biotiques différents (CHAPITRES 1, 2, 4), et ne sont pas indépendantes (CHAPITRES 1, 3, 4). Cela remet en question l'utilisation des mesures agrégées de multifonctionnalité (méthodes par calcul de la moyenne, ou *averaging method*, Hector *et al.* (2007), Gamfeldt & Roger (2017), CHAPITRE 1, méthodes des seuils, Byrnes *et al.* (2014), Manning *et al.* (2018)). En effet, en s'affranchissant de la nature multivariée des différentes fonctions écosystémiques, les indices de multifonctionnalité classiques perdent l'information sur les réponses individuelles des fonctions écosystémiques aux variations de l'environnement et de la communauté multi-trophique (Dooley *et al.*, 2015). Ils ignorent également les corrélations entre fonctions, et donc perdent l'information sur leurs synergies (Dooley *et al.*, 2015). Cependant, les approches adoptées dans ma thèse (modélisation indépendante des fonctions et de la multifonctionnalité, CHAPITRES 1, 2, approche non-dirigée dans le CHAPITRE 4) n'apportent que des solutions partielles à ce problème. D'une part, la modélisation indépendante des fonctions permet de conserver l'information sur les réponses spécifiques des différentes fonctions écosystémiques à l'environnement et à la communauté multi-trophique (CHAPITRES 1, 2), mais ne permet pas d'avoir une compréhension holistique du fonctionnement de l'écosystème. De plus, elle intègre mal les interdépendances entre les fonctions. D'autre part, bien que les approches non-dirigées telles que le *graphical lasso* permettent de prendre en compte les interdépendances entre fonctions et de s'affranchir de la vision hiérarchique environnement-biodiversité-fonctionnement (CHAPITRE 4), elles ne permettent ni de prédire le fonctionnement des écosystèmes dans l'espace géographique, ni de réellement comprendre l'aspect temporel et directionnel des rétroactions entre environnement, biodiversité et fonctionnement, ni d'avoir une vision intégrée du fonctionnement des écosystèmes. Une méthode spatialement explicite, qui prenne également en compte des séries temporelles, et qui soit à la fois intégrative, multivariée et prédictive sera donc nécessaire pour modéliser les multiples fonctions écosystémiques ensemble dans l'espace.

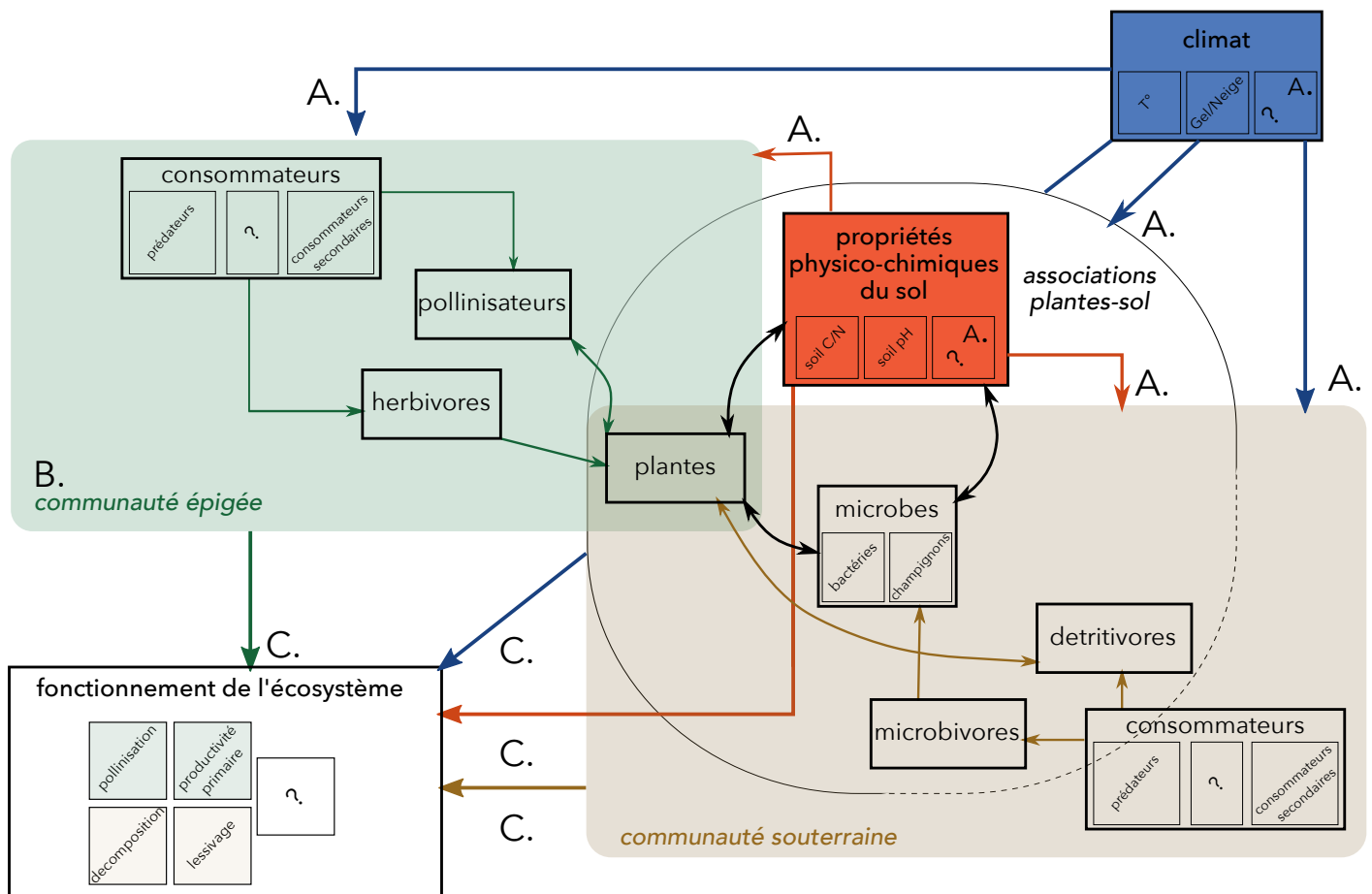
IV. Perspectives à court terme : futures pistes de progression pour la recherche sur le lien entre environnement, biodiversité et fonctionnement des écosystèmes.

Je pense que pour atteindre l'objectif de la prédiction du fonctionnement des écosystèmes dans l'espace, il faudra i/ continuer à prendre en compte la variation spatiale des conditions environnementales, en particulier celles des propriétés physico-chimiques du sol, ii/ continuer à améliorer la prise en compte des interactions trophiques et non-trophiques, qui permettent de comprendre les effets indirects des différents groupes trophiques sur les fonctions écosystémiques et d'identifier des groupes clefs pour le fonctionnement des écosystèmes, iii/ garder la nature multivariée des différentes fonctions écosystémiques qui peuvent être régulées par l'environnement et les groupes trophiques de façons différentes.

Cependant, la synthèse de mes travaux de thèse soulève également de nouvelles questions, qui sont des perspectives à court terme pour la recherche sur le lien entre environnement, biodiversité et fonctionnement des écosystèmes. Notamment, i/ *Quels sont les meilleurs prédicteurs environnementaux des différents groupes trophiques ? Quelle est l'importance des effets en cascade de ces prédicteurs environnementaux sur le fonctionnement des écosystèmes ? Peuvent-ils se compenser ?* ; ii/ *Comment intégrer les réseaux épigés, notamment les herbivores, qui ont souvent été identifiés comme des groupes trophiques clefs du fonctionnement, pour prédire les fonctions écosystémiques ?* ; iii/ *Comment modéliser les interdépendances et rétroactions entre les différentes fonctions écosystémiques ? Peut-on trouver une méthode à la fois spatialement explicite, holistique, multivariée et prédictive pour modéliser les multiples fonctions écosystémiques ensemble dans l'espace ?*

Dans cette partie, en m'appuyant sur un schéma à la fois issu des résultats présentés dans cette thèse, des résultats et analyses annexes que j'ai réalisés dans ma thèse mais non présentés ici, et des questions qui en émergent (Figure 9), je discute certaines des perspectives qui me semblent particulièrement intéressantes. Ce schéma, que j'ai pensé pour qu'il soit facilement adaptable dans un modèle d'équations structurelles, peut être vu comme une feuille de route des perspectives de ma thèse, mais également comme un objectif accessible à court terme.

Figure 9 (à droite) | Perspectives à court terme. A., B., et C. renvoient aux perspectives discutées dans les paragraphes correspondants de ce IV. La boîte bleue représente le climat. On peut y intégrer des variables agrégées sur différentes périodes temporelles, selon les groupes trophiques (A.). À ce niveau hiérarchique, on pourrait également intégrer les perturbations anthropiques (ex. polluants, destruction des habitats naturels). La boîte rouge représente les conditions abiotiques du sol. On peut y intégrer différentes variables importantes pour différents groupes trophiques (A.). Je l'ai descendue d'un niveau hiérarchique pour que le climat puisse avoir un impact sur toutes les variables impliquées dans les associations plantes-sol (encart arrondi). Les encarts verts et bruns correspondent respectivement aux communautés épigées et souterraines. Intégrer les communautés épigées (B.), mais également les fonctions de surface qui leurs sont associées (ex. pollinisation, voir l'encart du fonctionnement des écosystèmes) dans nos modèles constitue une perspective importante. Enfin, les flèches associées à l'encart du fonctionnement des écosystèmes représentent l'importance de garder l'aspect multivarié du fonctionnement des écosystèmes, tout en ayant une approche holistique du fonctionnement (C.).



A. Améliorer la connaissance des prédicteurs environnementaux des différents groupes trophiques.

De façon intéressante, ma thèse suggère que les variations des conditions environnementales influencent différemment les groupes trophiques (ex. leur composition). L'effet de l'environnement se répercute donc sur le fonctionnement différemment selon les groupes trophiques. Or, afin de pouvoir quantifier correctement ces effets indirects de l'environnement, et identifier les cas où ils se compensent, il est essentiel de bien connaître les prédicteurs environnementaux des différents groupes trophiques (Figure 9). Dans le cadre de ma thèse, nous avons toujours choisi les prédicteurs environnementaux avec une vision assez plante-centrée, en particulier les prédicteurs climatiques. Par exemple, le GDD et le FDD, que j'ai utilisés de façon récurrente, ont été calculés sur la base de la saison de végétation des plantes. Nous les avons modélisés à l'échelle des plots (CHAPITRE 3, Figure 1), et moyennés sur des périodes temporelles qui correspondent à une estimation du temps nécessaire pour que le climat puisse modifier la composition des communautés végétales (CHAPITRE 3). Cependant, les différents groupes trophiques du sol ont des écologies très différentes des plantes, et très différentes entre elles. En particulier, ils ont des niches abiotiques, des cycles (et des durées) de vie, des tailles, et des ressources très différents (INTRO., Box 2). Les variations environnementales qui influencent leurs physiologies et leur survie se situent donc vraisemblablement à des échelles spatiales et temporelles différentes de celles des plantes. Cela est d'autant plus vrai que le sol est un milieu extrêmement hétérogène, caractérisé par des micro-gradients climatiques et des conditions physico-chimiques

du sol très différentes à des échelles qui vont de celle des pores à celle du plot (Coleman, Callaham, & Crossley, 2018; Hooper *et al.*, 2000; Lavelle, 2004).

Il y a donc un véritable intérêt à réaliser des modèles de distribution d'espèces pour les organismes du sol. Ces modèles de distribution d'espèces devront s'attacher à répondre à trois grandes questions :

i/ *Quels sont les meilleurs prédicteurs, climatiques et édaphiques, des différents taxa du sol ?* Pour répondre à cette question, les modèles devront s'appuyer sur les connaissances de l'écologie des différents taxa, et tester différentes variables nécessaires à leur survie et à leur physiologie, qui pourraient bien décrire la niche abiotique des taxa du sol (Travail de thèse d'Irène Calderon-Sanou).

ii/ *Quelle est l'échelle spatiale à laquelle ces prédicteurs ont du sens ?* Afin de déceler l'échelle spatiale la plus pertinente, les modèles devront développer des échantillonnages emboîtés, de l'échelle de la carotte de sol à celle du paysage.

iii/ *Quelle est l'échelle temporelle à laquelle ces prédicteurs ont du sens ?* Spécialement intéressante dans le cas des prédicteurs climatiques, cette question nécessitera sûrement de combiner des données des modèles climatiques avec celles mesurées par des thermomètres sur le terrain. Cela permettra de comparer des moyennes sur différentes périodes temporelles, de la journée qui précédait l'échantillonnage à une période de trente ans, comme utilisée pour les plantes.

En utilisant les techniques moléculaires (*eDNA metabarcoding*) à des échelles taxonomiques assez larges (ex. famille), on pourra sûrement dans les prochaines années affiner la connaissance des prédicteurs environnementaux des organismes du sol. En outre, cela permettra d'améliorer la définition des différents groupes trophiques, en ajoutant des informations sur leur niche abiotique dans les critères de regroupement (Boulangéat *et al.*, 2012; Winemiller, Fitzgerald, Bower, & Pianka, 2015). C'est d'ailleurs ce que nous faisons dans un article en préparation, qui propose un cadre conceptuel pour améliorer et standardiser la construction des groupes trophiques et fonctionnels des organismes du sol (Capowiez *et al.*, 2021, in prep.). Dans cette collaboration, j'ai participé à la conceptualisation et à la rédaction du manuscrit.

B. Prendre en compte les réseaux épigés.

Au cours des vingt dernières années, de plus en plus de publications, notamment d'expériences et de revues, ont montré que les communautés et les fonctions écosystémiques en surface et dans le sol (*aboveground-belowground communities and ecosystem functions*) sont intrinsèquement liées, et que les rétroactions entre ces deux systèmes ont des implications importantes pour la structure des communautés et le fonctionnement des écosystèmes (De Deyn & Van Der Putten, 2005; Hooper *et al.*, 2000; Van Der Putten *et al.*, 2009; Wardle *et al.*, 2004). La plupart des mécanismes proposés pour expliquer la relation entre le sous-système du sol et sur le sous-système sur le sol sont indirects, via les plantes (De Deyn & Van Der Putten, 2005; Hooper *et al.*, 2000). Cela a conduit une grande partie des publications à se concentrer sur un sous-ensemble du système (Van Der Putten *et al.*, 2009). Notamment, une grande partie des études qui se sont intéressées aux associations spatiales entre les communautés épigées et souterraines à larges échelles se sont concentrées sur les liens entre plantes et microbes (Boeddinghaus *et al.*, 2019; Buzzard *et al.*, 2019; de Vries *et al.*, 2012).

Cependant, les caractéristiques des communautés de plantes, notamment leurs traits fonctionnels et leur composition, peuvent être influencées par leurs interactions avec les organismes de plusieurs niveaux trophiques supérieurs, que cela soit au-dessus du sol ou dans le sol (Van Der Putten *et al.*, 2009; Van Der Putten, Vet, Harvey, & Wäckers, 2001). En outre, la réponse des communautés de plantes au réseau trophique épigé peut se transférer au réseau du sol, et modifier sa composition et ses interactions (et *vice versa*), ce qui peut avoir des conséquences indirectes sur les fonctions écosystémiques (Figure 9, Van Der Putten *et al.*, 2009; Wardle & Bardgett, 2002). Par exemple, les herbivores et les décomposeurs des racines peuvent modifier la productivité primaire nette et modifier la composition chimique de la biomasse végétale, influençant ainsi l'herbivorie, le parasitisme, la pollinisation et la production de graines en surface (Poveda, Steffan-Dewenter, Scheu, & Tscharrntke, 2005). Il semble donc essentiel de considérer plusieurs niveaux trophiques sous et sur le sol pour bien comprendre les liens indirects, via les plantes, entre les réseaux épigés et les réseaux du sol, et leurs conséquences sur le fonctionnement des écosystèmes (Figure 9).

De plus, les interactions trophiques au sein du sous-système sur le sol ont majoritairement été décrites séparément de celles au sein du sous-système du sol. Les liens directs entre les groupes trophiques épigés et souterrains sont très peu documentés, et généralement ignorés. Cependant, dans le cas où les conditions environnementales imposent un stress important, comme en haute-altitude, où les sols peuvent être très peu épais et où les ressources sont beaucoup plus rares, on peut s'attendre à ce qu'il existe des interactions directes entre les réseaux sur et dans le sol. Par exemple, on peut s'attendre à ce que certains prédateurs épigés (ex. les araignées) se nourrissent à la fois dans les communautés souterraines et épigées, avec des effets sur les fonctions écosystémiques beaucoup plus directs qu'à des altitudes plus basses, où la stratification verticale du sol conduit sûrement les deux sous-systèmes à être beaucoup plus séparés (modularité⁶ élevée, Peralta, Frost, Didham, Rand, & Tylianakis (2017), Newman (2006)).

⁶ La modularité désigne une mesure de la structure des réseaux, qui mesure la force de la division des nœuds du réseau en modules, aussi appelés groupes, clusters ou communautés (Newman, 2006)

Malgré cela, nous nous sommes restreints dans le cadre de ma thèse à l'intégration des plantes et des organismes du sol dans la modélisation du lien environnement-biodiversité-fonctionnement. En effet, les données d'ADN environnemental issues de carottes de sol ne sont pas adaptées pour étudier la biodiversité épigée. C'est notamment dû au fait que le matériel génétique des organismes épigés n'est disponible que sous forme de traces, en très petites quantités, dans les carottes de sol. De plus, les bases de références pour certains taxa très importants dans le compartiment épigé (ex. insectes) ont été développées majoritairement pour des marqueurs plus longs que ceux usuellement utilisés avec la technique d'ADN environnemental (ex. CO1). Par conséquent, les séquences associées aux organismes épigés ont généralement été supprimées au cours du processus de nettoyage bio-informatique, et exclues de la plupart de mes travaux de thèse.

En parallèle de mes travaux de thèse, j'ai échantillonné les organismes épigés sur la plupart des gradients d'altitudes qui sont inclus dans les CHAPITRES 2, 3 et 4, et réaliser des extractions sur les échantillons complets (i.e. sur les individus, Box 4). La généralisation de ce genre de techniques, combinées à l'échantillonnage plus classique des carottes de sol, pourrait permettre à l'avenir d'étendre facilement les questions abordées dans ma thèse aux communautés épigées (Box 4).

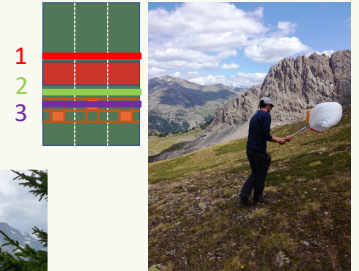
Box 4 (à droite) | Étapes réalisées au cours de cette thèse et perspectives pour intégrer les communautés épigées à nos modèles du lien environnement-biodiversité-fonctionnement des écosystèmes.

Intégrer les communautés épigées dans la modélisation du lien environnement-biodiversité-fonctionnement des écosystèmes

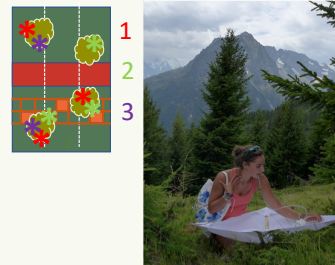
- **Quel est l'impact de la biodiversité multi-trophique de surface sur les différentes fonctions de l'écosystème et sur la multifonctionnalité ?** H1. La biodiversité multi-trophique de surface influence les fonctions de surface (ex. productivité, pollinisation) plus fortement que les fonctions du sol (ex. décomposition, Jing 2015, Soliveres 2016 (b), Wagg 2014)
- **Quelle est l'importance relative de la biodiversité multi-trophique de surface et de celle du sol sur le fonctionnement des écosystèmes ?** H2. Elles ont des relations différentes avec la multifonctionnalité (Soliveres 2016 (b), Wagg 2014). H3. L'importance dépend plutôt de la distance des groupes trophiques aux plantes que de leur place par rapport au sol, par ex. décomposeurs et herbivores sont plus importants que les autres groupes (Soliveres 2016 (a), Lindeman 1942)
- **Les structures des réseaux trophiques (à l'échelle des groupes trophiques) de surface et du sol répondent-elles de manière similaire à l'environnement ?** H4. La structure des réseaux trophiques du sol est moins impactée que celle des réseaux de surface. H5. Les réseaux du sol répondent plus aux variables édaphiques qu'au climat et *vice versa* pour les réseaux de surface (CHAPITRES 1, 2, 3, 4).
- **Comment le couplage des réseaux de surface et du sol change-t-il le long d'un gradient de stress ?** H6. Le couplage est plus important (connectivité plus élevée) quand les conditions environnementales sont plus stressantes

Pour échantillonner les communautés, j'ai pu disposer de l'observatoire ORCHAMP. Sur les mêmes gradients et sites que ceux utilisés pour les autres chapitres de cette thèse, j'ai échantillonné la communauté de surface avec trois techniques adaptées pour décrire la faune épigée :

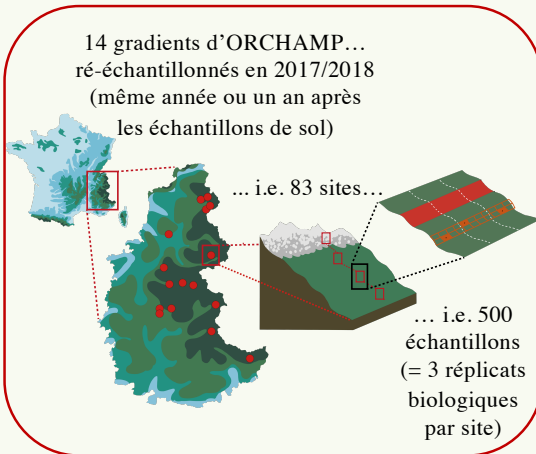
A. Transects de filet-faucheur pour les prairies →



← B. Parapluie japonais pour les branches basses



C. Aspirateur sur une surface standardisée pour la litière →



A. Extraction de l'ADN des échantillons de filet-faucheur et de parapluie japonais.

Les individus échantillonnés ont été directement plongés dans l'éthanol, puis séchés par silicagel. L'avantage de cette technique de conservation est qu'elle permet d'extraire l'ADN intracellulaire des individus dans les échantillons, via la protéinase K dans un tampon de lyse cellulaire (résultat de tests expérimentaux réalisés durant ma thèse mais non présentés ici). Le reste des étapes (amplification, séquençage) rejoint le protocole utilisé pour les échantillons de sol, mais la qualité de l'ADN intracellulaire permet d'utiliser des marqueurs plus longs (ex. CO1), qui permettent de mieux cibler et identifier la faune épigée, et qui sont mieux référencés pour les arthropodes (majorité de la faune épigée échantillonnée).

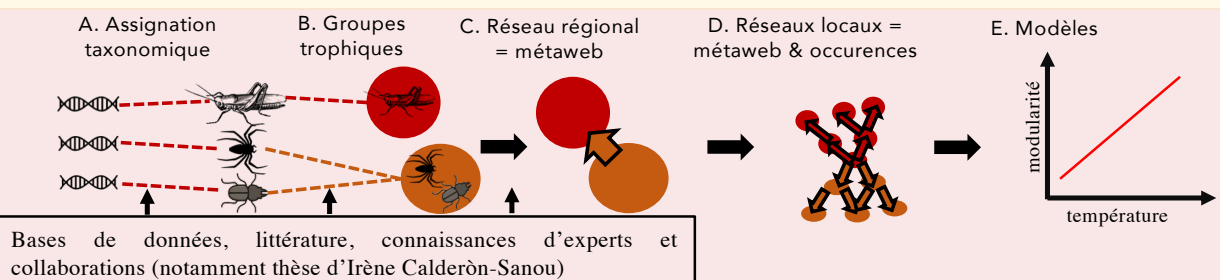
B. Extraction de l'ADN des échantillons de l'aspirateur.

Les échantillons issus de l'aspirateur sont de vrais échantillons de litière : ils contiennent peu d'individus complets et beaucoup de matière organique végétale. Ils sont difficiles à trier, et l'utilisation d'un tampon de lyse cellulaire dans ce cas conduit à la libération de beaucoup d'ADN intracellulaire des plantes et d'inhibiteurs de la PCR, ce qui perturbe l'étape d'amplification de l'ADN (résultat de tests expérimentaux réalisés durant ma thèse mais non présentés ici).

Nous avons donc utilisé le protocole d'extraction de l'ADN extracellulaire pour ces échantillons (i.e. le même que celui des échantillons de sol des chapitres antérieurs).

Extraction, amplification et séquençage de l'ADN

Ce qu'il reste à faire



C. Aller vers une modélisation multivariée de la multifonctionnalité

Nous avons montré que les différentes fonctions écosystémiques ont des prédicteurs différents. Ma thèse souligne également l'importance des rétroactions entre propriétés du sol, plantes, microbes et fonctions écosystémiques (CHAPITRES 1, 3, 4, Boeddinghaus *et al.*, 2019; Legay *et al.*, 2014; Wardle & Bardgett, 2002). De plus, il est probable que ce type de rétroactions impliquent également des niveaux trophiques plus hauts, sous et sur le sol (De Deyn & Van Der Putten, 2005; Hooper *et al.*, 2000; Van Der Putten *et al.*, 2009, 2001; Wardle *et al.*, 2004). Ces rétroactions, qui se produisent à des échelles de temps différentes, sont difficiles à modéliser au sein de modèles d'équations structurelles (bien qu'ils puissent intégrer des boucles dans certaines circonstances, Grace (2016)). De plus, elles sont ignorées par les indices de multifonctionnalité classiques (Byrnes, Gamfeldt, *et al.*, 2014; Byrnes, Lefcheck, *et al.*, 2014). Cependant, elles peuvent se traduire à un instant $-t$ par des corrélations et synergies entre les différentes fonctions écosystémiques, qu'il devient urgent de considérer lorsqu'on cherche à prédire la multifonctionnalité dans l'espace géographique.

Une modélisation multivariée spatialement explicite des fonctions de l'écosystème pourrait permettre de modéliser explicitement les corrélations et les synergies entre les fonctions de l'écosystème. Dooley *et al.* ont déjà proposé une telle approche (Dooley *et al.*, 2015), avec l'extension multivariée du modèle diversité-interactions de Kirwan *et al.* (2009). Dans le modèle diversité-interactions multivarié (*Multivariate Diversity - Interactions model*), la comparaison des composantes du modèle pour les différentes fonctions de l'écosystème permet de quantifier la réponse de chaque fonction, selon des prédicteurs tels que l'identité des espèces, les interactions entre espèces ou les variables environnementales. De plus, ce modèle inclut automatiquement les corrélations entre les fonctions. Il permet d'avoir une compréhension holistique du fonctionnement des écosystèmes, et il résume la capacité de l'écosystème à assurer plusieurs fonctions simultanément. Entre d'autres termes, il permet d'évaluer la multifonctionnalité de l'écosystème (Manning *et al.*, 2018). Adapté aux groupes trophiques, le modèle de Dooley *et al.* (2015) constitue une perspective intéressante et facilement applicable à court terme pour la prédiction et la cartographie du fonctionnement des écosystèmes dans l'espace.

Par ailleurs, il ne serait pas difficile d'intégrer une modélisation multivariée du fonctionnement au sein des modèles d'équations structurelles (Figure 9). En effet, les méthodes récemment développées par Bill Shipley et John Lefcheck permettent d'intégrer des modèles linéaires mixtes généralisés dans les modèles d'équations structurelles (Lefcheck, 2016; Shipley, 2000, 2016). Il est donc maintenant possible de modéliser toutes les fonctions en même temps (i.e. comme une seule variable réponse, avec l'identité des fonctions en facteur aléatoire), au sein d'un modèle d'équations structurelles qui intégrerait les interactions entre groupes trophiques et les différents prédicteurs environnementaux (Figure 9). Cette perspective me semble particulièrement intéressante, car elle permettrait de bénéficier des avantages du modèle diversité-interactions multivarié, tout en conservant l'aspect hiérarchique des modèles d'équations structurelles.

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Annexes



Installation de nouvelles placettes sur le gradient d'Argentière (ARG)

1. Annexes du chapitre 1

Figure S1 | Principal Component Analysis run for all scaled environmental variables. The first axis summarizes climatic and topographical conditions whereas the second axis is related to soil conditions.

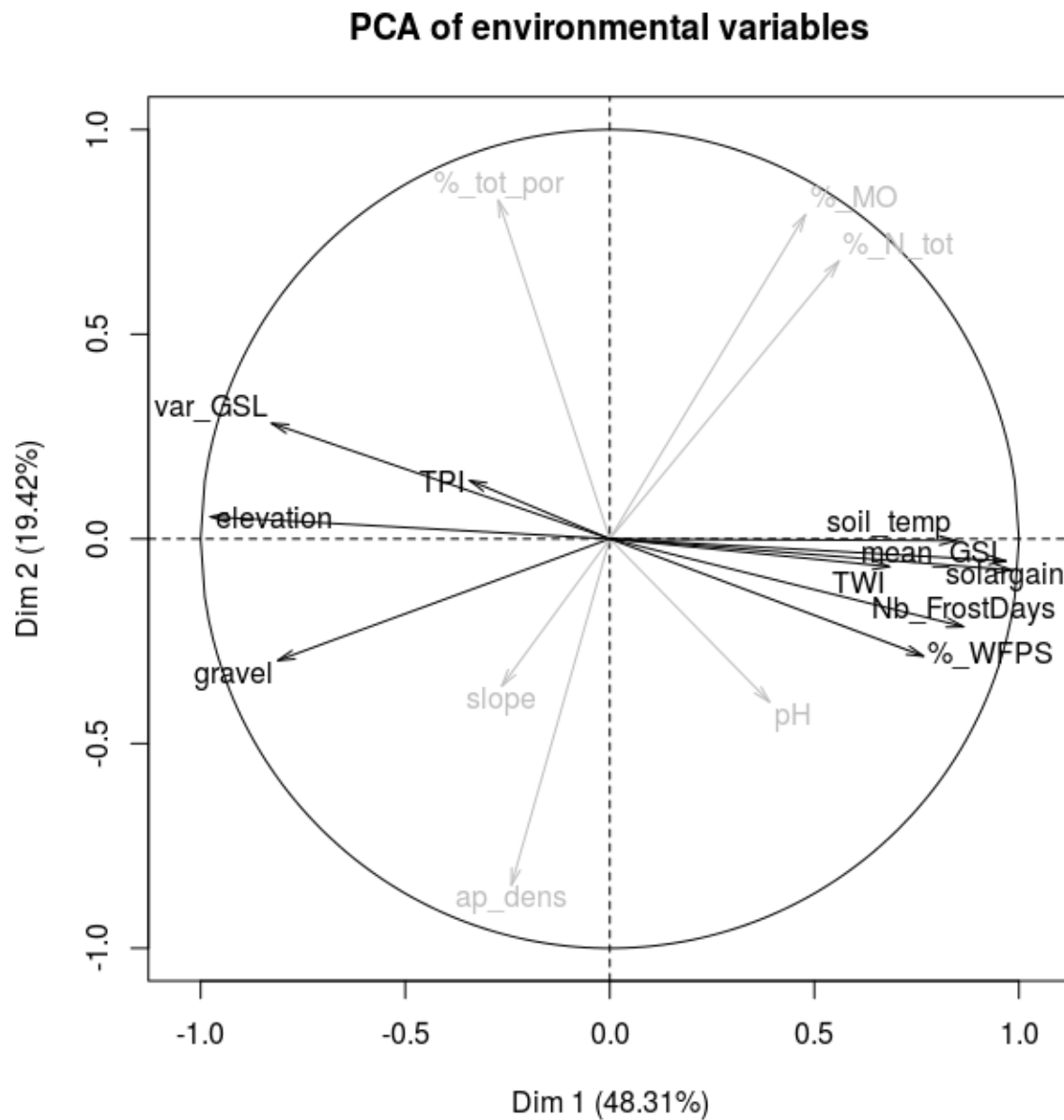


Figure S2 | Correlations of each ecosystem function (i.e. productivity, N-cycling, N-leaching) with the multifunctionality metric. Significant pairwise Pearson correlation tests are represented by stars.

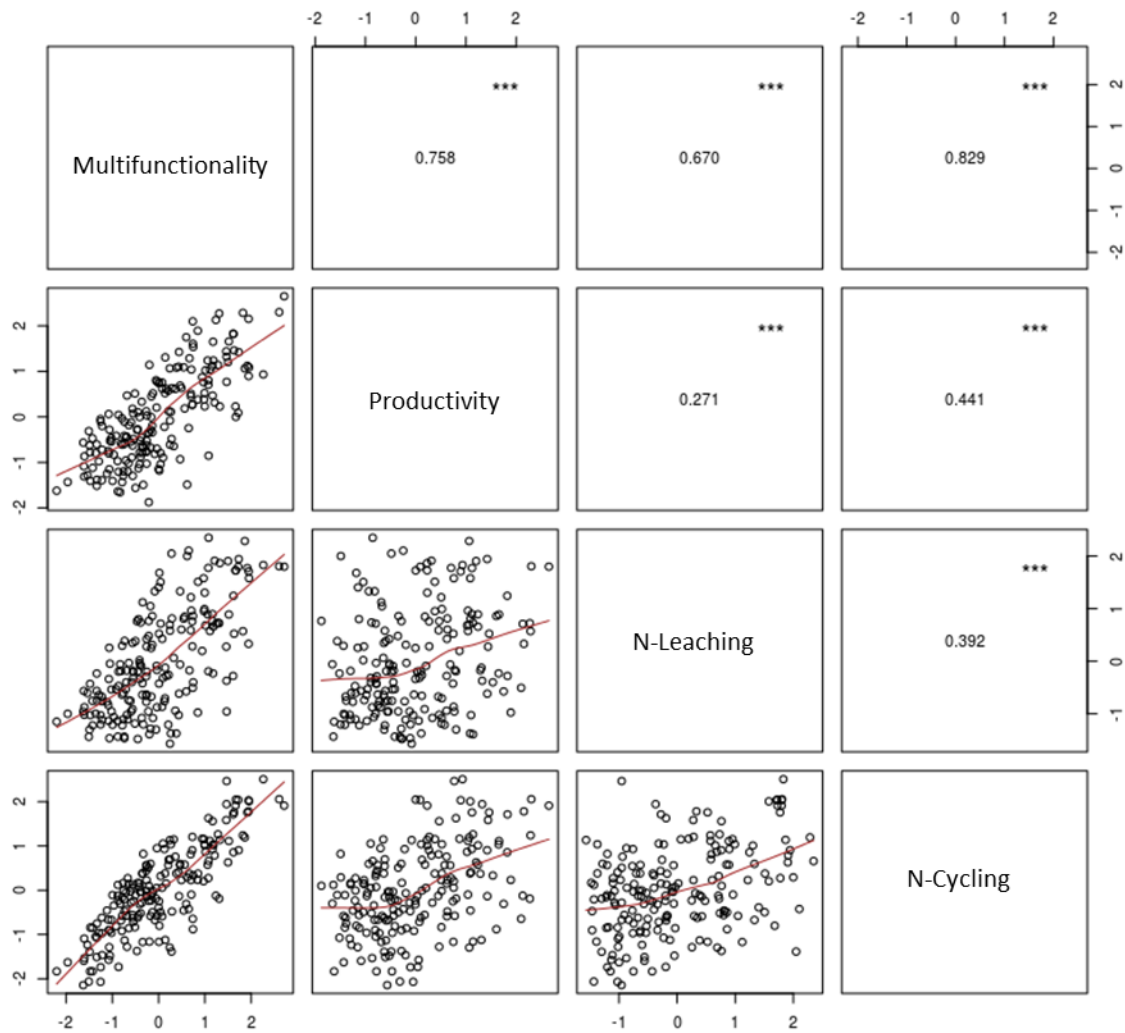
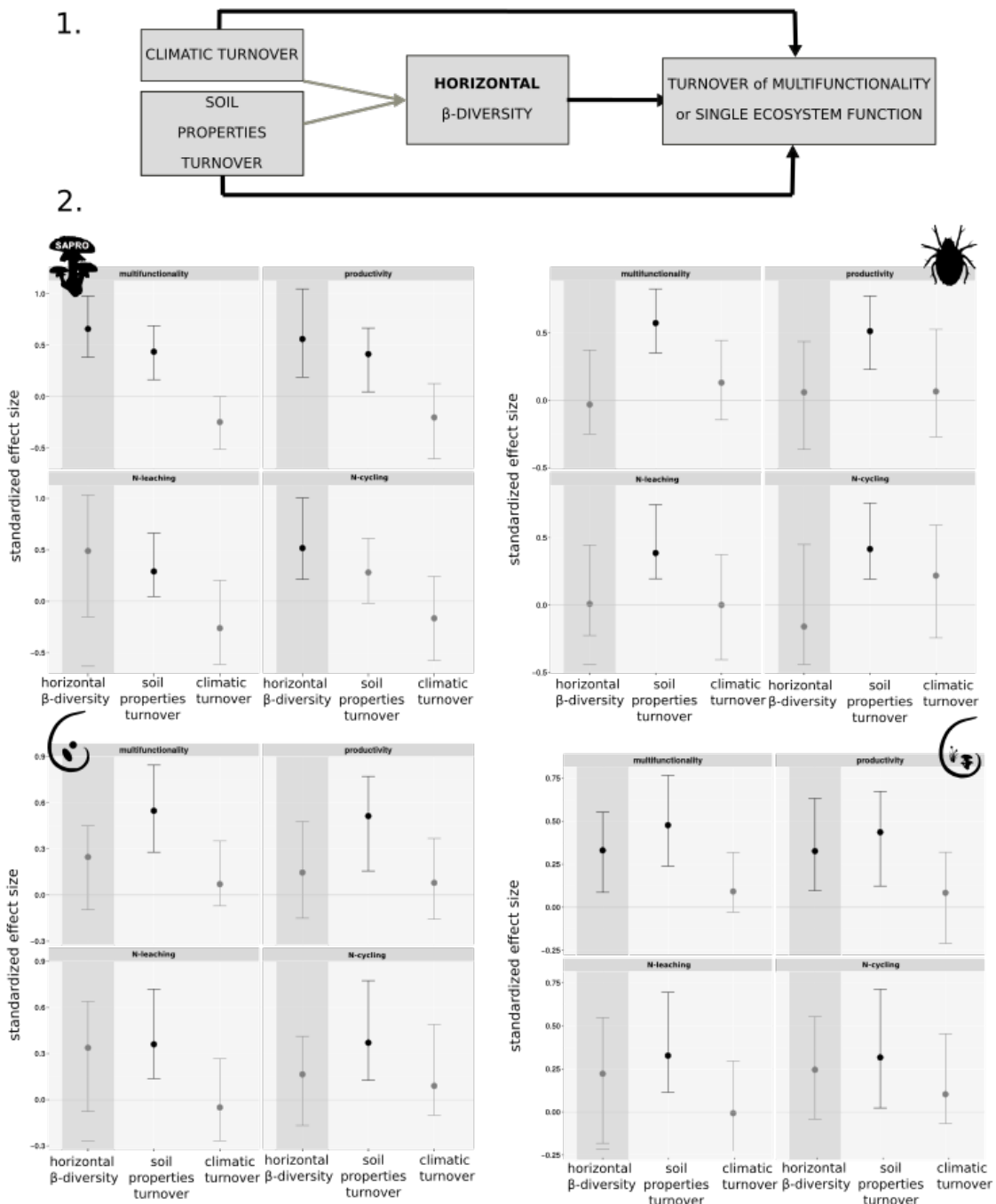


Figure S3 | Comparison of horizontal β -diversity direct effect, soil turnover direct effect and climatic turnover direct effect on the turnover of multiple ecosystem functions. 1. Structure of the tested path analyses. The standardized coefficients which correspond to the bold arrows are further represented in the second part of the figure. 2. Direct standardized effects of the horizontal β -diversity of each trophic group on multifunctionality or single ecosystem functions (conditioned by climate and soil), and direct effects of soil and climatic turnover.



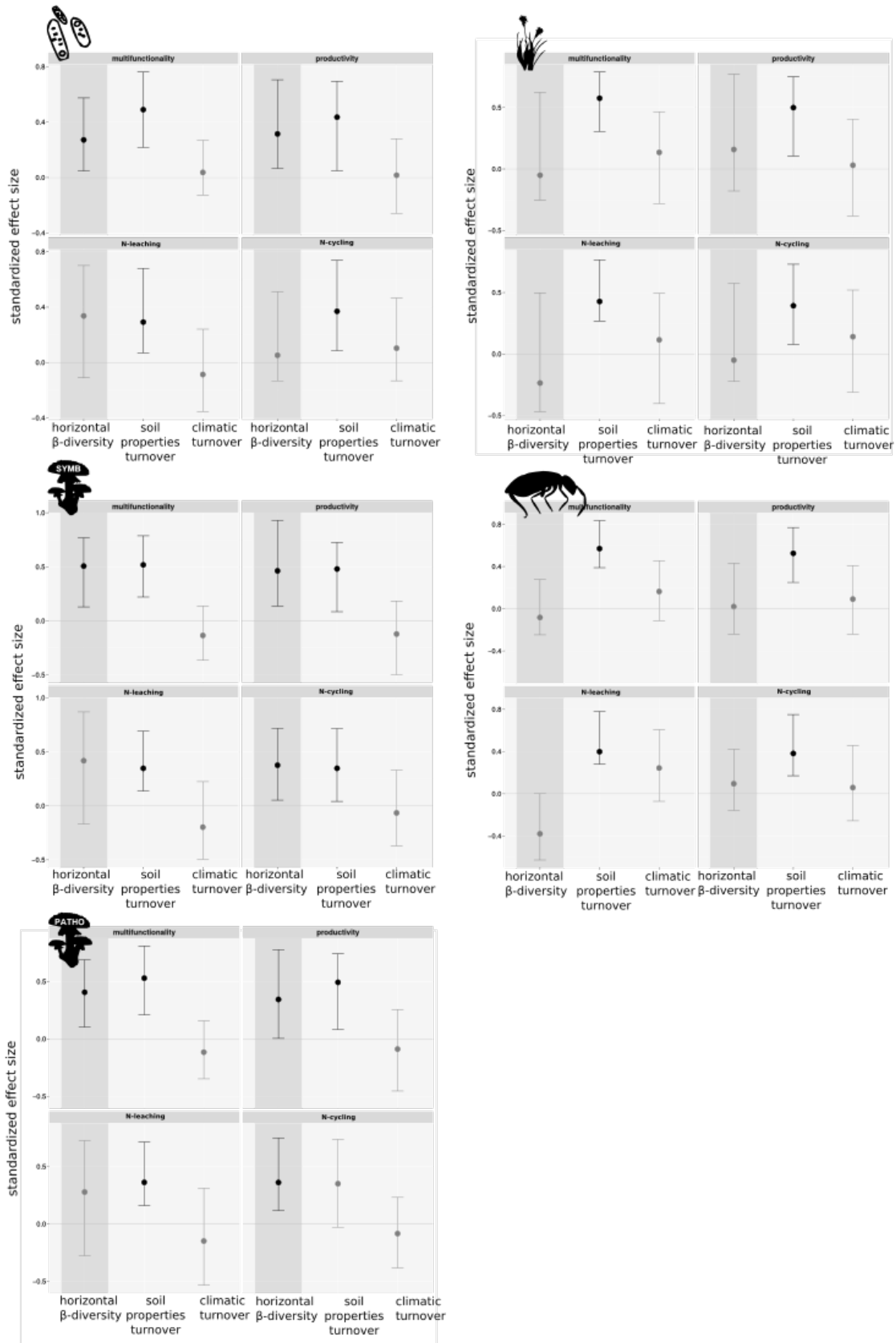


Figure S4 | Final minimal path model highlighting the direct and indirect effects of climate and soil turnover on turnover of productivity under consideration of combined horizontal β -

diversities of the trophic groups that were found important in the independent horizontal β -diversities models (Figure 5). The size of the arrows is proportional to the size of the associated standardized path coefficients (only for significant paths). Dotted grey lines represent non-significant paths. Paths with double arrows represent correlations.

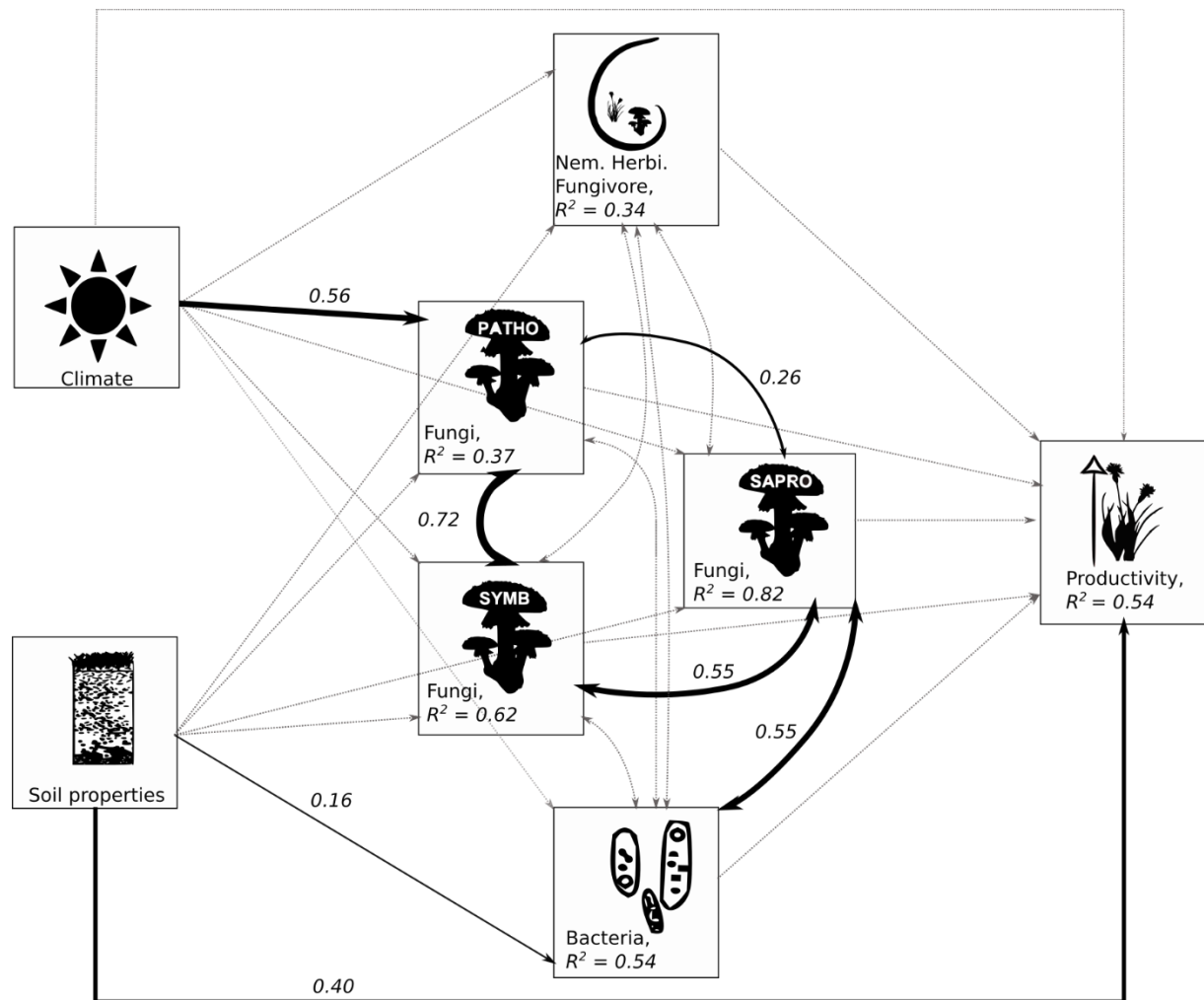


Figure S5 | Final minimal path model highlighting the direct and indirect effects of climate and soil turnover on turnover of N-cycling under consideration of combined horizontal β -diversities of the trophic groups that were found important in the independent horizontal β -diversities models (Figure 5). The size of the arrows is proportional to the size of the associated standardized path coefficients (only for significant paths). Dotted grey lines represent non-significant paths. Paths with double arrows represent correlations.

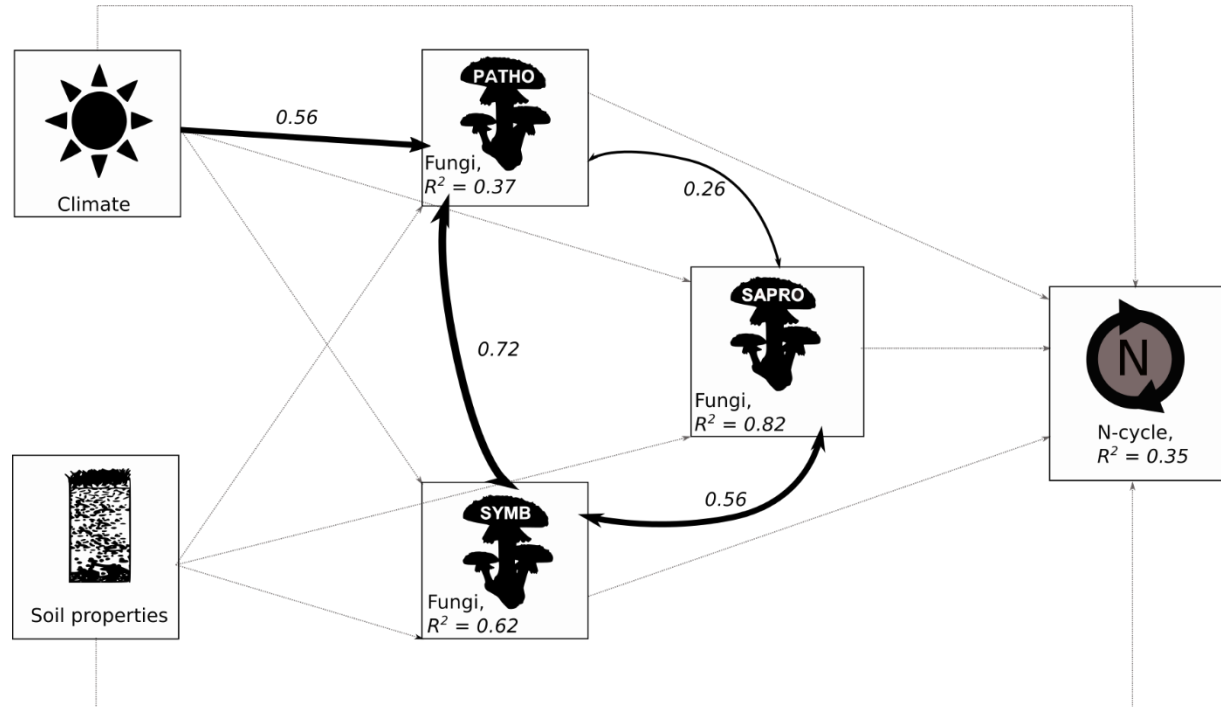


Figure S6 | Environmental turnover effects on the horizontal β -diversity of each trophic groups, the total multi-trophic β -diversity and the vertical β -diversity. 1. Structure of the tested path analyses. The standardized coefficients which correspond to the bold arrows are further represented in the second part of the figure. 2. Direct standardized effects of the climatic and soil turnover on the horizontal β -diversity of each trophic group, the total multi-trophic β -diversity and the vertical β -diversity.

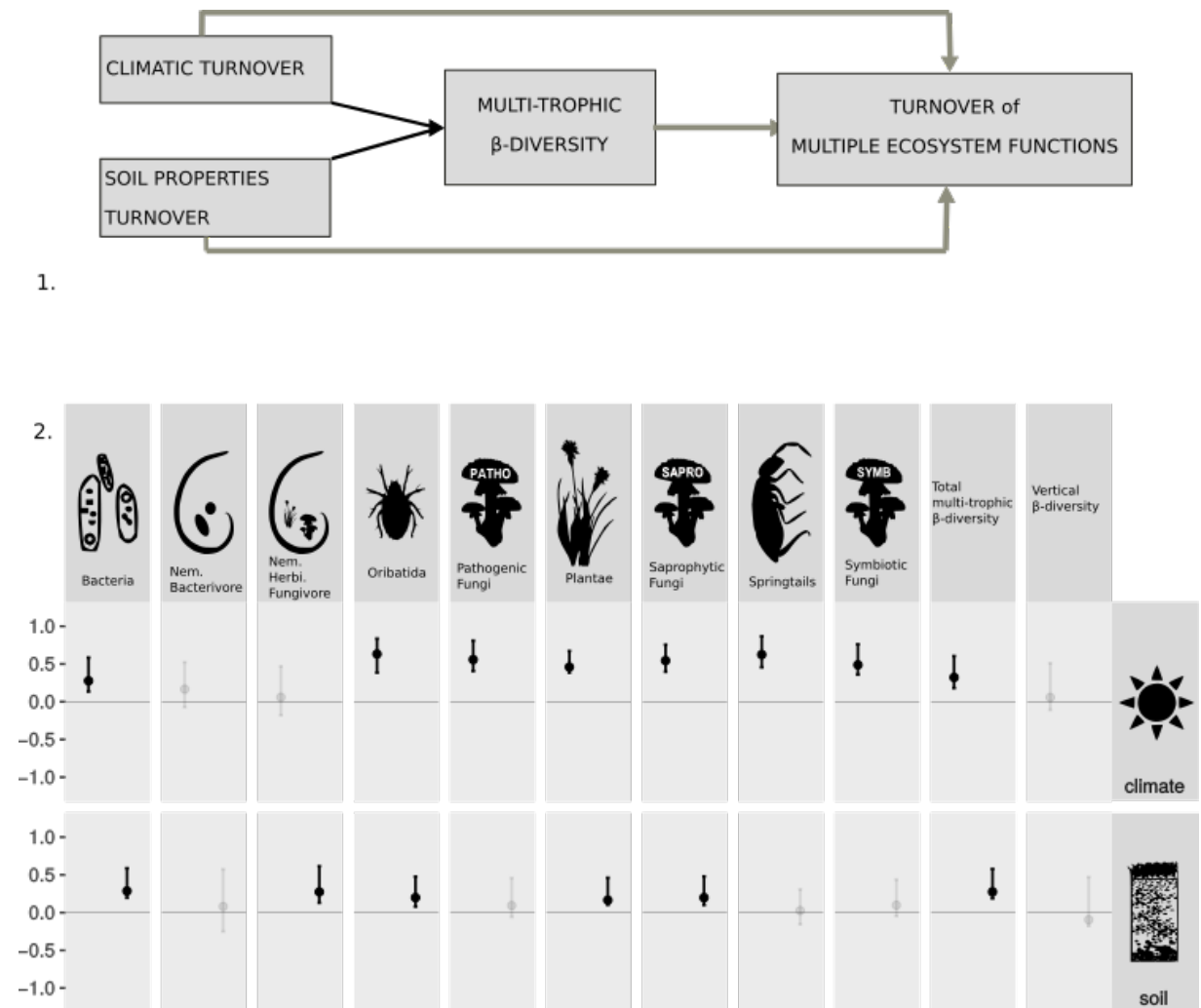
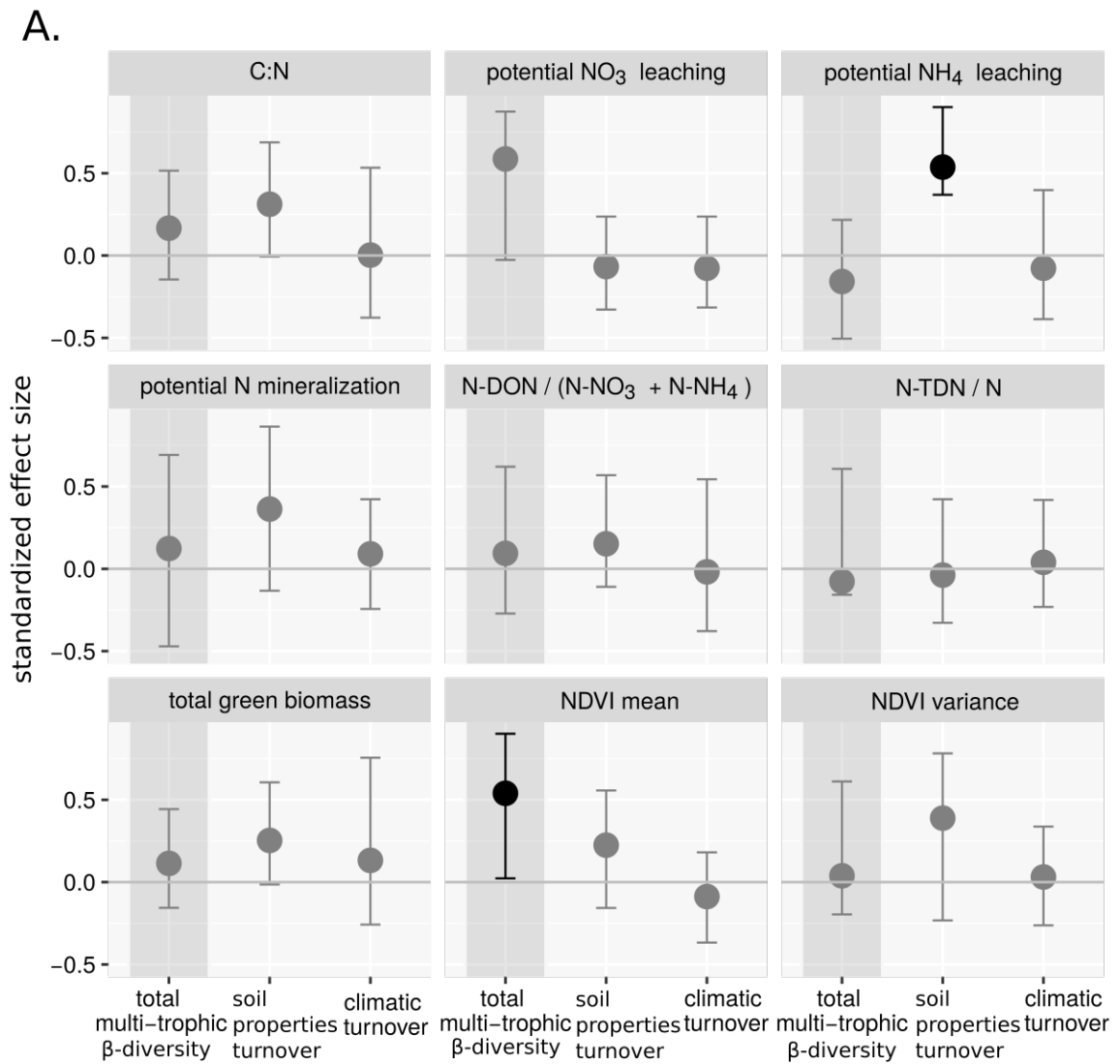
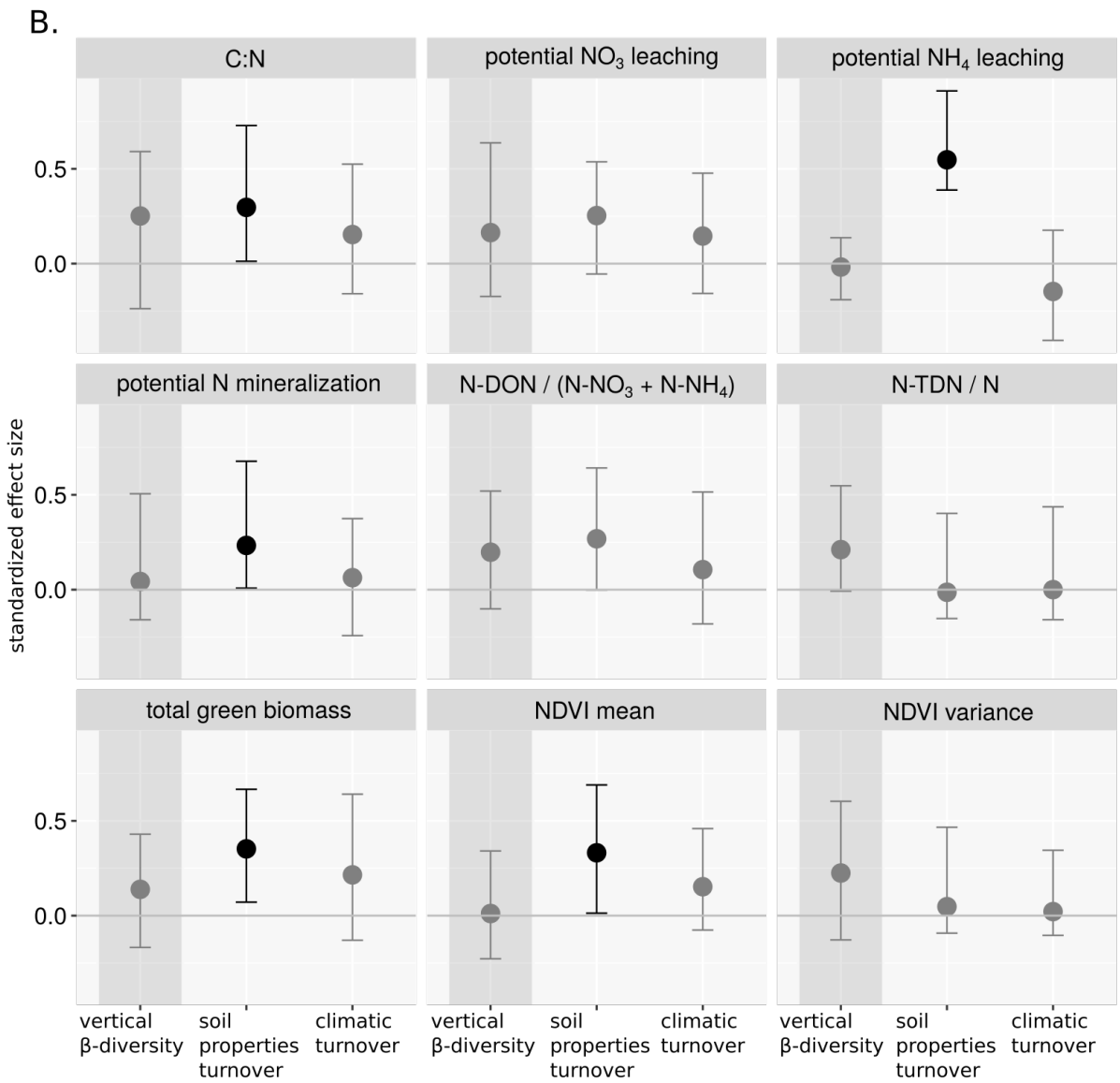
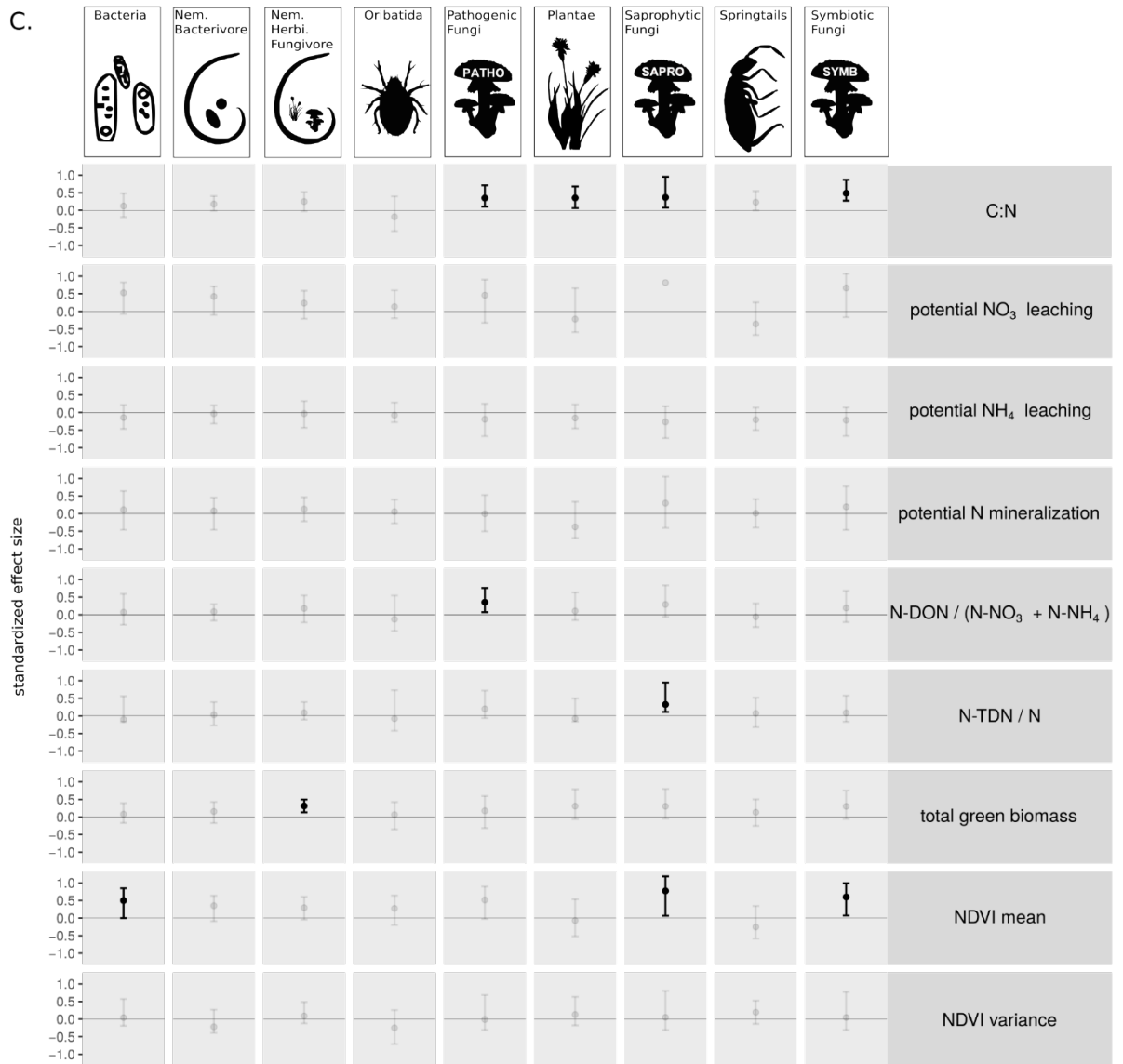


Figure S7 | Analyses for all ecosystem functions. A. Analyses for total multi-trophic β -diversity. B. Analyses for vertical β -diversity. C. Analyses for horizontal β -diversity. D. Final integrated path analyses for mean of NDVI and C/N.

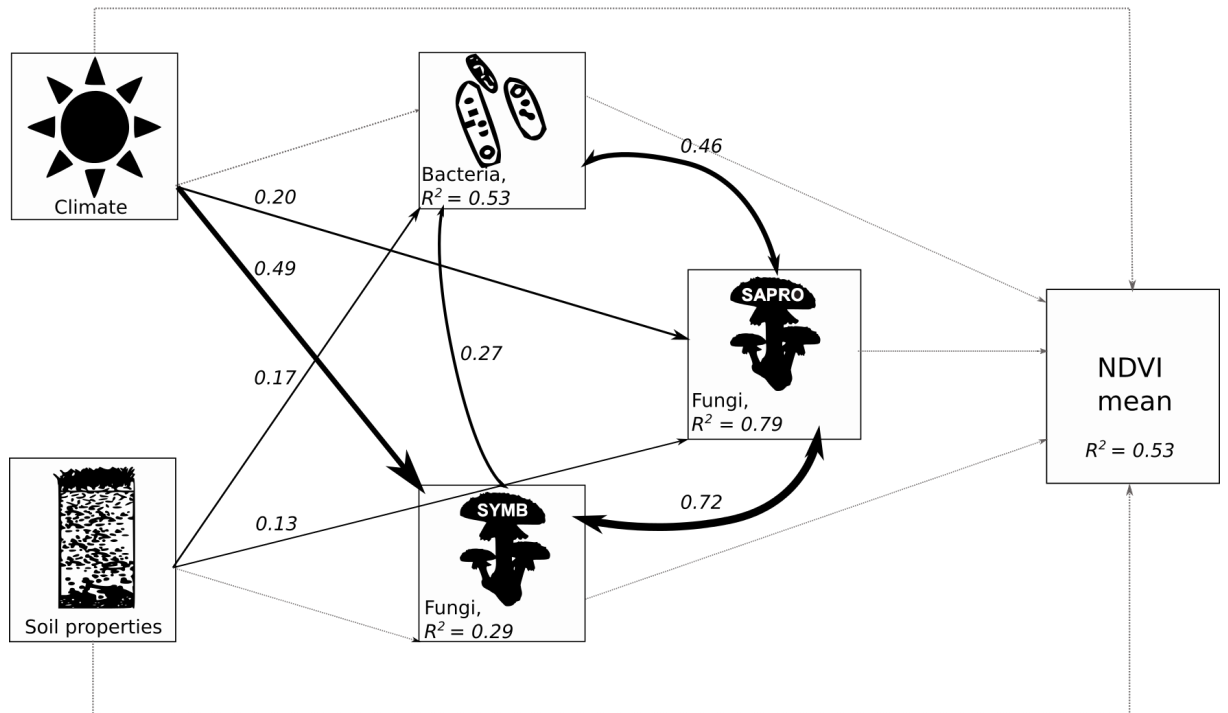




C.



D.



E.

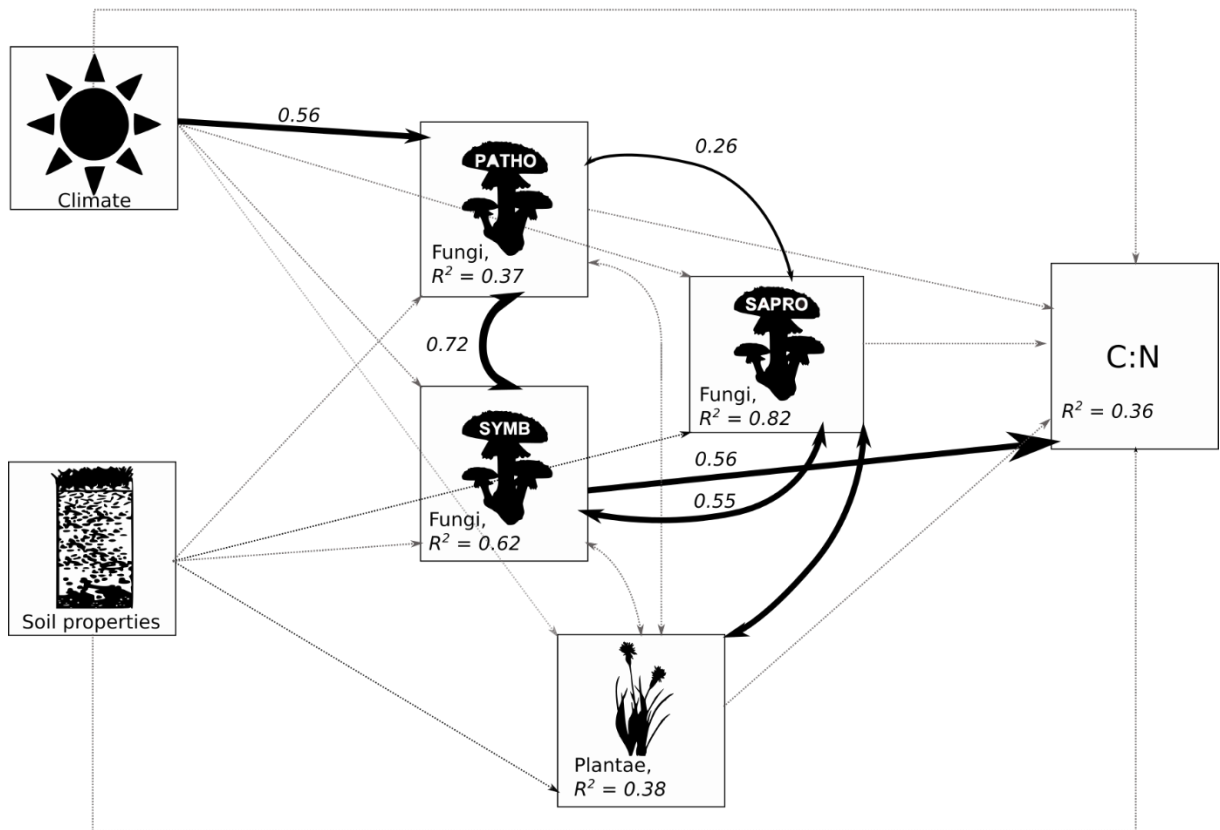


Figure S8 | Partial regressions for each ecosystem function against total α -diversity and horizontal α -diversity of each trophic group.

residuals of individual ecosystem functions

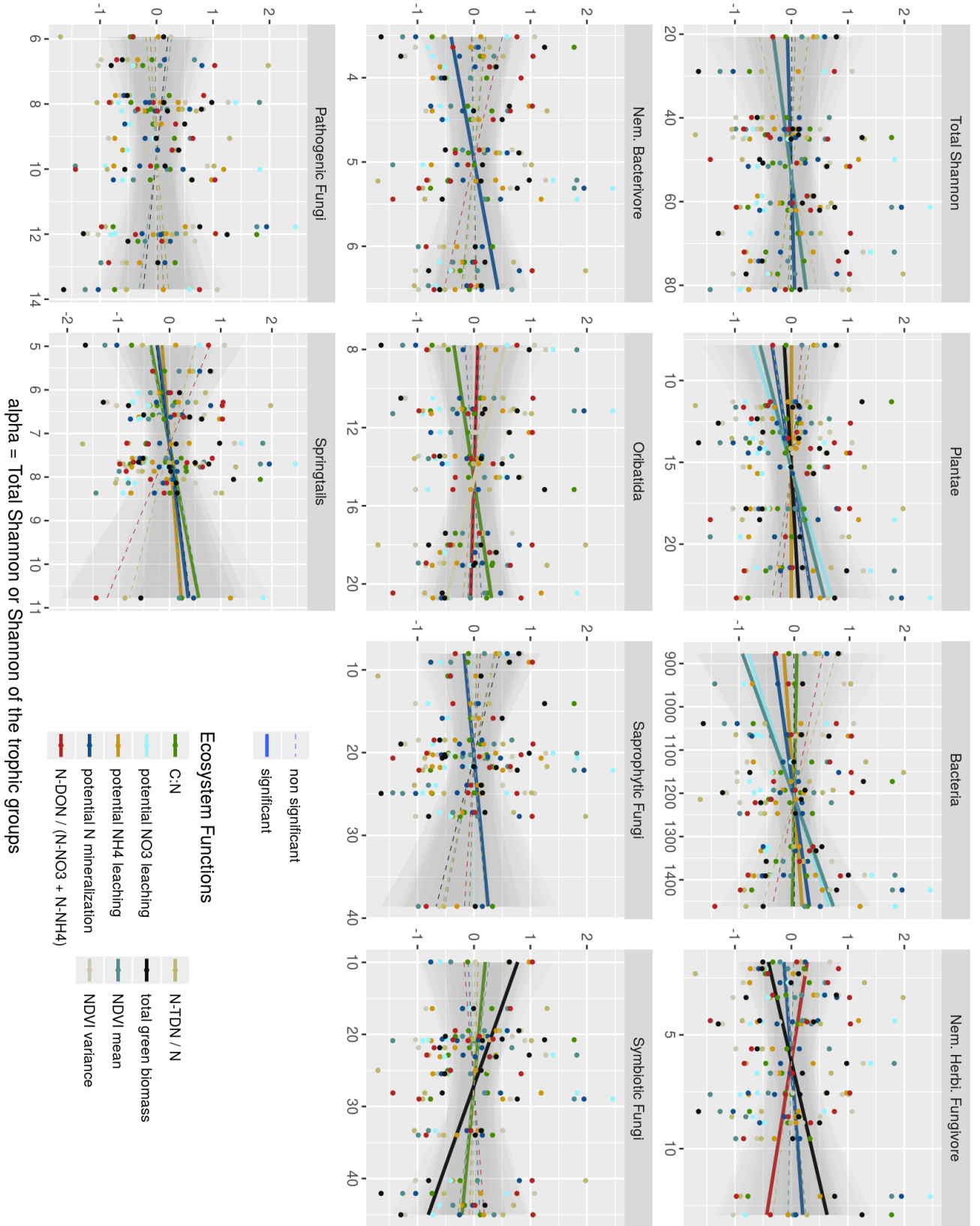


Table S1 | Standardized path coefficients and corresponding confidence intervals for the final minimal path model for multifunctionality, productivity and N-cycle (figure 6, figure S4, figure S5), and for single ecosystem functions (C:N, mean NDVI, figure S6-D&E) .

Path	Path coefficient	Confidence interval's lower bound	Confidence interval's upper bound	Path model for :
Bacteria ~ climate	-7.607E-02	-3.258E-01	2.007E-01	multifunctionality
Bacteria ~ soil	1.630E-01	2.740E-03	3.778E-01	multifunctionality
Nem.Herbi.Fungivore ~ climate	-2.684E-01	-7.720E-01	1.497E-01	multifunctionality
Nem.Herbi.Fungivore ~ soil	1.869E-01	-7.189E-02	4.479E-01	multifunctionality
Saprophytic.Fungi ~ climate	1.317E-01	-1.884E-02	3.875E-01	multifunctionality
Saprophytic.Fungi ~ soil	1.204E-01	-7.368E-03	2.706E-01	multifunctionality
Symbiotic.Fungi ~ climate	8.447E-02	-1.333E-01	3.987E-01	multifunctionality
Symbiotic.Fungi ~ soil	3.074E-02	-9.997E-02	2.264E-01	multifunctionality
Pathogenic.Fungi ~ climate	5.584E-01	4.040E-01	8.096E-01	multifunctionality
Pathogenic.Fungi ~ soil	9.391E-02	-5.739E-02	4.596E-01	multifunctionality
multifunctionality ~ climate	-2.190E-01	-4.809E-01	3.759E-02	multifunctionality
multifunctionality ~ soil	4.485E-01	1.741E-01	6.802E-01	multifunctionality
multifunctionality ~ Bacteria	-1.477E-01	-3.956E-01	1.377E-01	multifunctionality
multifunctionality ~ Nem.Herbi.Fungivore	9.654E-02	-8.978E-02	2.839E-01	multifunctionality
multifunctionality ~ Saprophytic.Fungi	6.667E-01	2.769E-01	1.156E+00	multifunctionality
multifunctionality ~ Symbiotic.Fungi	1.353E-01	-3.021E-01	4.223E-01	multifunctionality
multifunctionality ~ Pathogenic.Fungi	-1.128E-01	-3.761E-01	1.939E-01	multifunctionality
Bacteria ~ Nem.Herbi.Fungivore	-4.316E-03	-1.027E-01	1.572E-01	multifunctionality
Bacteria ~ Saprophytic.Fungi	5.543E-01	2.123E-01	1.002E+00	multifunctionality
Bacteria ~ Symbiotic.Fungi	3.459E-01	-8.534E-02	5.914E-01	multifunctionality
Bacteria ~ Pathogenic.Fungi	-2.103E-01	-4.886E-01	2.063E-01	multifunctionality
Nem.Herbi.Fungivore ~ Saprophytic.Fungi	2.371E-01	-3.968E-01	9.081E-01	multifunctionality
Nem.Herbi.Fungivore ~ Symbiotic.Fungi	4.091E-01	-3.509E-02	9.313E-01	multifunctionality
Nem.Herbi.Fungivore ~ Pathogenic.Fungi	-1.522E-03	-3.894E-01	4.303E-01	multifunctionality
Saprophytic.Fungi ~ Symbiotic.Fungi	5.494E-01	2.645E-01	7.088E-01	multifunctionality
Saprophytic.Fungi ~ Pathogenic.Fungi	2.600E-01	6.349E-02	4.378E-01	multifunctionality
Symbiotic.Fungi ~ Pathogenic.Fungi	7.226E-01	4.226E-01	9.460E-01	multifunctionality
Bacteria ~ climate	-7.607E-02	-3.266E-01	2.013E-01	productivity
Bacteria ~ soil	1.630E-01	1.016E-03	3.769E-01	productivity
Nem.Herbi.Fungivore ~ climate	-2.684E-01	-7.781E-01	1.509E-01	productivity
Nem.Herbi.Fungivore ~ soil	1.869E-01	-7.269E-02	4.484E-01	productivity
Saprophytic.Fungi ~ climate	1.317E-01	-1.914E-02	3.858E-01	productivity
Saprophytic.Fungi ~ soil	1.204E-01	-6.132E-03	2.715E-01	productivity
Symbiotic.Fungi ~ climate	8.447E-02	-1.342E-01	3.988E-01	productivity
Symbiotic.Fungi ~ soil	3.074E-02	-1.001E-01	2.269E-01	productivity
Pathogenic.Fungi ~ climate	5.584E-01	4.019E-01	8.097E-01	productivity
Pathogenic.Fungi ~ soil	9.391E-02	-5.572E-02	4.600E-01	productivity
productivity ~ climate	-1.509E-01	-5.933E-01	2.264E-01	productivity
productivity ~ soil	4.010E-01	4.315E-02	6.698E-01	productivity
productivity ~ Bacteria	-1.068E-03	-3.931E-01	2.660E-01	productivity
productivity ~ Nem.Herbi.Fungivore	1.306E-01	-5.309E-02	3.916E-01	productivity
productivity ~ Saprophytic.Fungi	4.227E-01	-1.350E-01	1.137E+00	productivity
productivity ~ Symbiotic.Fungi	1.488E-01	-2.912E-01	6.839E-01	productivity
productivity ~ Pathogenic.Fungi	-9.932E-02	-5.362E-01	3.139E-01	productivity
Bacteria ~ Nem.Herbi.Fungivore	-4.316E-03	-1.037E-01	1.572E-01	productivity
Bacteria ~ Saprophytic.Fungi	5.543E-01	2.136E-01	9.952E-01	productivity
Bacteria ~ Symbiotic.Fungi	3.459E-01	-8.729E-02	5.904E-01	productivity
Bacteria ~ Pathogenic.Fungi	-2.103E-01	-4.867E-01	2.065E-01	productivity
Nem.Herbi.Fungivore ~ Saprophytic.Fungi	2.371E-01	-3.912E-01	9.146E-01	productivity
Nem.Herbi.Fungivore ~ Symbiotic.Fungi	4.091E-01	-3.895E-02	9.361E-01	productivity
Nem.Herbi.Fungivore ~ Pathogenic.Fungi	-1.522E-03	-3.916E-01	4.284E-01	productivity
Saprophytic.Fungi ~ Symbiotic.Fungi	5.494E-01	2.626E-01	7.072E-01	productivity
Saprophytic.Fungi ~ Pathogenic.Fungi	2.600E-01	6.555E-02	4.383E-01	productivity
Symbiotic.Fungi ~ Pathogenic.Fungi	7.226E-01	4.228E-01	9.461E-01	productivity
Saprophytic.Fungi ~ climate	1.317E-01	-1.918E-02	3.881E-01	N-cycling
Saprophytic.Fungi ~ soil	1.204E-01	-6.467E-03	2.712E-01	N-cycling
Symbiotic.Fungi ~ climate	8.447E-02	-1.328E-01	4.025E-01	N-cycling
Symbiotic.Fungi ~ soil	3.074E-02	-1.002E-01	2.271E-01	N-cycling
Pathogenic.Fungi ~ climate	5.584E-01	4.060E-01	8.077E-01	N-cycling
Pathogenic.Fungi ~ soil	9.391E-02	-5.657E-02	4.565E-01	N-cycling
N-cycling ~ climate	-1.709E-01	-5.920E-01	1.892E-01	N-cycling
N-cycling ~ soil	2.834E-01	-5.128E-02	6.336E-01	N-cycling
N-cycling ~ Saprophytic.Fungi	4.903E-01	-2.709E-01	1.298E+00	N-cycling
N-cycling ~ Symbiotic.Fungi	-2.006E-03	-5.966E-01	5.590E-01	N-cycling
N-cycling ~ Pathogenic.Fungi	4.068E-02	-3.828E-01	5.887E-01	N-cycling
Saprophytic.Fungi ~ Symbiotic.Fungi	5.494E-01	2.638E-01	7.071E-01	N-cycling
Saprophytic.Fungi ~ Pathogenic.Fungi	2.600E-01	6.606E-02	4.388E-01	N-cycling
Symbiotic.Fungi ~ Pathogenic.Fungi	7.226E-01	4.215E-01	9.447E-01	N-cycling

Path	Path coefficient	Confidence interval's lower bound	Confidence interval's upper bound	Path model for :
Plantae ~ climate	2.853E-01	-9.311E-02	5.144E-01	C_N
Plantae ~ soil	1.505E-01	-5.346E-03	3.699E-01	C_N
Saprophytic.Fungi ~ climate	1.317E-01	-1.942E-02	3.848E-01	C_N
Saprophytic.Fungi ~ soil	1.204E-01	-6.422E-03	2.710E-01	C_N
Symbiotic.Fungi ~ climate	8.447E-02	-1.335E-01	4.004E-01	C_N
Symbiotic.Fungi ~ soil	3.074E-02	-1.007E-01	2.273E-01	C_N
Pathogenic.Fungi ~ climate	5.584E-01	4.036E-01	8.081E-01	C_N
Pathogenic.Fungi ~ soil	9.391E-02	-5.751E-02	4.591E-01	C_N
C_N ~ climate	-2.189E-01	-7.304E-01	3.098E-01	C_N
C_N ~ soil	2.995E-01	-5.226E-02	6.688E-01	C_N
C_N ~ Plantae	2.361E-01	-3.187E-01	5.242E-01	C_N
C_N ~ Saprophytic.Fungi	-1.686E-01	-1.041E+00	6.627E-01	C_N
C_N ~ Symbiotic.Fungi	5.582E-01	1.589E-01	1.194E+00	C_N
C_N ~ Pathogenic.Fungi	-2.376E-02	-4.846E-01	4.672E-01	C_N
Plantae ~ Saprophytic.Fungi	-1.610E-01	-4.934E-01	5.579E-01	C_N
Plantae ~ Symbiotic.Fungi	1.927E-01	-3.338E-01	4.995E-01	C_N
Plantae ~ Pathogenic.Fungi	3.017E-01	-8.089E-02	7.370E-01	C_N
Saprophytic.Fungi ~ Symbiotic.Fungi	5.494E-01	2.650E-01	7.064E-01	C_N
Saprophytic.Fungi ~ Pathogenic.Fungi	2.600E-01	6.654E-02	4.378E-01	C_N
Symbiotic.Fungi ~ Pathogenic.Fungi	7.226E-01	4.237E-01	9.467E-01	C_N
Bacteria ~ climate	-1.085E-01	-3.282E-01	1.558E-01	ndvi_mean
Bacteria ~ soil	1.674E-01	8.900E-03	3.732E-01	ndvi_mean
Saprophytic.Fungi ~ climate	1.950E-01	3.878E-02	4.601E-01	ndvi_mean
Saprophytic.Fungi ~ soil	1.282E-01	2.242E-02	2.800E-01	ndvi_mean
Symbiotic.Fungi ~ climate	4.880E-01	3.603E-01	7.626E-01	ndvi_mean
Symbiotic.Fungi ~ soil	9.860E-02	-4.478E-02	4.364E-01	ndvi_mean
ndvi_mean ~ climate	-3.193E-01	-6.661E-01	7.088E-02	ndvi_mean
ndvi_mean ~ soil	2.067E-01	-1.747E-01	5.427E-01	ndvi_mean
ndvi_mean ~ Bacteria	1.377E-01	-3.735E-01	3.501E-01	ndvi_mean
ndvi_mean ~ Saprophytic.Fungi	5.931E-01	-1.276E-01	1.390E+00	ndvi_mean
ndvi_mean ~ Symbiotic.Fungi	9.072E-02	-4.470E-01	6.768E-01	ndvi_mean
Bacteria ~ Saprophytic.Fungi	4.630E-01	1.932E-01	8.830E-01	ndvi_mean
Bacteria ~ Symbiotic.Fungi	2.732E-01	-7.376E-02	5.674E-01	ndvi_mean
Saprophytic.Fungi ~ Symbiotic.Fungi	7.171E-01	3.951E-01	8.205E-01	ndvi_mean

2. Annexes du chapitre 2

Appendix S1 | ORCHAMP: Spatio-temporal observatory of biodiversity and ecosystem functioning of mountains' socio-ecosystems

1. Brief description

ORCHAMP is a long-term observatory of mountain ecosystems aiming to observe, understand and model biodiversity and ecosystem functioning over space and time. It relies on the active involvement of local actors, managers and researchers with the objective to better safeguard the contribution of biodiversity to human society.

ORCHAMP is built around multiple elevational gradients representative of the pedo-climatic environmental space of the French Alps (Fig. S1-A2). In this article we used 18 gradients (Fig. S1-A2). Each gradient consists of 4 to 8 permanent plots distributed regularly each 200 m of altitude, from down the valley to the top (Fig S1-A1). They are resampled on average every 5 years using a rotating sampling scheme. In this article no resampling data were used. Measures include physical properties (soil temperature, physicochemical, and pedology), biodiversity estimates (botanical surveys, multi-trophic biodiversity using soil environmental DNA, tree growth, deadwood in forests), ecosystem functions (productivity, enzymatic activities, soil organic matter) and human uses. Data are open-access and synthesized following GEOBON recommendations on Essential Biodiversity Variables. Specific data used in this paper are described in the main text.

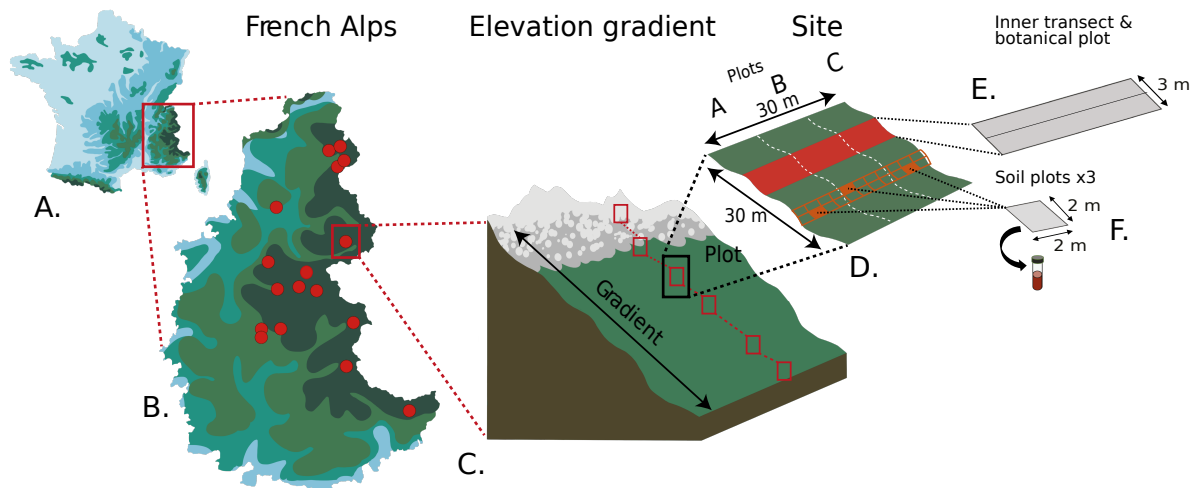
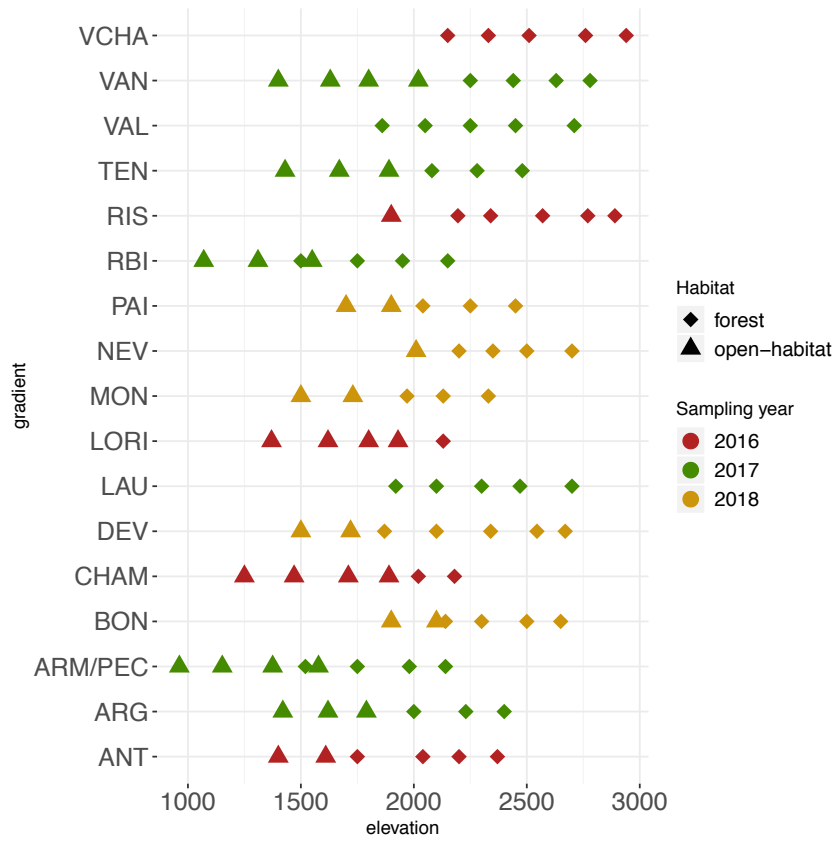
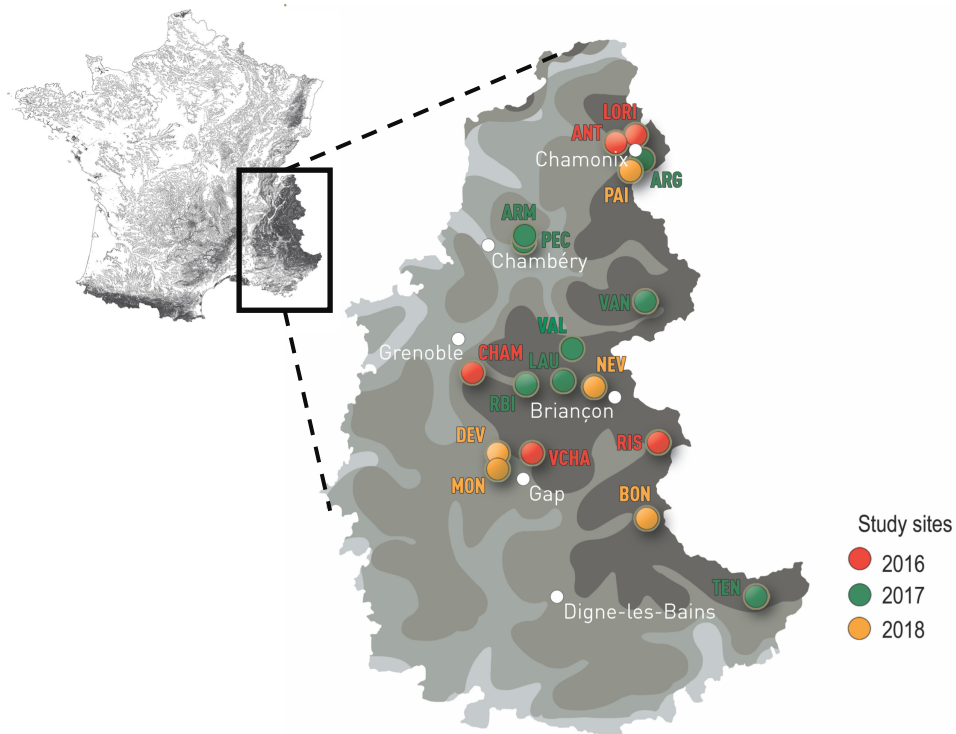


Figure S1-A1: Experimental design of the ORCHAMP long-term observatory. (A) Location of the observatory in the French Alps, (B) location of the 18 elevation gradients, (C) example of the elevation distribution along the gradient, (D) sampling design of one site, (red area, E) represents the inner transect of the site, (F) represents the area where the soil sampling is done on three 2×2 m subplots randomly chosen for each year of sampling.



A.



B.

Figure S1-A2: Overview of the 18 gradients of ORCHAMP used in this study: Repartition of the elevations and habitat per gradient (A), location of gradients (B), names and year of sampling (A, B).

2. Institutions involved in ORCHAMP

ORCHAMP is a consortium gathering a large range of actors: national and regional park managers, botanical conservatory experts, natural area conservatory managers, association, researchers from universities and research institutions. Most of the actors involved in ORCHAMP are also members of the LTSER Zone Atelier Alpes. The project is led by the LECA (Laboratoire d'Écologie Alpine - <https://leca.osug.fr/>), located in Grenoble. For additional information please visit our website: <https://orchamp.osug.fr/home> or contact us: orchamp@univ-grenoble-alpes.fr

- **LECA** - Laboratoire d'Écologie Alpine; Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, Laboratoire d'Ecologie Alpine, Grenoble, France
<https://leca.osug.fr/>
- **EDYTEM** - Environnements, DYnamiques et TErritoires de la Montagne; CNRS, Univ. Savoie Mont Blanc, Pôle Montagne, Le Bourget du Lac, France
<http://edytem.univ-savoie.fr/>
- **INRAE LESSEM** - Laboratoire Ecosystèmes et Sociétés En Montagne; Univ. Grenoble Alpes, INRAE, UR LESSEM, Grenoble, France
<https://www.irstea.fr/fr/recherche/unites-de-recherche/lessem>
- **IMBE** - Institut Méditerranéen de la Biodiversité et d'Écologie marine et continentale; CNRS Aix Marseille Univ., France
<https://www.imbe.fr/l-unite.html>
- **SAJF** - Station Alpine Joseph Fourier; Univ. Grenoble Alpes, CNRS, Grenoble, France
<https://www.jardinalpindulautaret.fr/>
- **CEN** - Centre d'Études de la Neige; Univ. Grenoble Alpes, Université de Toulouse, Météo-France, CNRS, Centre National de Recherches Météorologiques, Grenoble, France
<https://www.umr-cnrm.fr/spip.php?rubrique85>
- **INRAE ECODIV** - Laboratoire Etude et Compréhension de la bioDIVERSité; Univ. de Rouen Normandie, Rouen, France
<http://ecodiv.univ-rouen.fr/fr>
- **Laboratoire de Géologie de l'ENS**; CNRS-ENS, Univ. PSL, Paris, France
<http://www.geologie.ens.fr/spiplabocnrs/>
- **INRAE URFM**, UR Ecologie des Forêts Méditerranéennes; INRAE, Avignon, France
https://www6.paca.inra.fr/ecologie_des_forets_mediterraneennes
- **INRAE UEFM** - UE Entomologie et Forêt Méditerranéenne; INRAE, Avignon, France
https://www6.paca.inra.fr/entomologie_foret_med
- **CBN Alpin** - Conservatoire Botanique National Alpin
<http://www.cbn-alpin.fr/>
- **CBN Med** - Conservatoire Botanique National Méditerranéen de Porquerolles
<http://www.cbnmed.fr/src/prez.php>
- **PN des Ecrins** - Parc National des Ecrins & **RI du Lauvitel** - Réserve intégrale du Lauvitel
<http://www.ecrins-parcnational.fr/>
- **PN du Mercantour** - Parc National du Mercantour

- <http://www.mercantour-parcnational.fr/fr>
- **PN de la Vanoise** - Parc National de la Vanoise
<http://www.vanoise-parcnational.fr/fr>
- **PNR du massif des Bauges** - Parc Naturel Régional du massif des Bauges
<http://www.parcdesbauges.com/fr/>
- **PNR de Chartreuse** - Parc Naturel Régional de Chartreuse
<http://www.parc-chartreuse.net/>
- **PNR du Queyras** - Parc Naturel Régional du Queyras & **RN Ristolas-Mont-Viso** - Réserve Naturelle Nationale de Ristolas-Mont-Viso
<https://www.pnr-queyras.fr/>
- **ASTER** - Conservatoire d'espaces naturels de Haute-Savoie & **RN Sixt-Passy** - Réserve Naturelle de Sixt-Passy
<http://www.cen-haute-savoie.org/>
- **CREA** - Centre de Recherches sur les Écosystèmes d'Altitude
<https://creamontblanc.org/fr>
- **Natura 2000 Clarée**
<https://inpn.mnhn.fr/site/natura2000/FR9301499>
- **Natura 2000 Dévoluy-Durbon-Charance-Champsaur**
<http://hautes-alpes.n2000.fr/devoluy>
- **SMIGIBA** - Syndicat Mixte de Gestion Intercommunautaire du Buëch et de ses affluents
<http://www.smigiba.fr/>
- **Grenoble-Alpes Métropole**
<https://www.lametro.fr/>

3. ORCHAMP Consortium (contact persons are in italics)

- **LECA:** *Wilfried Thuiller, Amélie Saillard*, Louise Boulangeat, Manon Bounous, Irene Calderon-Sanou, Philippe Choler, Arnaud Foulquier, Ludovic Gielly, Priscilla Godfroy, Maya Gueguen, Nicolas Le Guillaume, Clément Lionnet, Camille Martinez-Almoyna, Gabin Piton, Julien Renaud, Tristan Ubaldi
- **INRAE LESSEM:** *Georges Kunstler*, Sophie Labonne, Pascal Tardif, Jean-Matthieu Monnet, Yoan Paillet
- **ECODIV:** *Lauric Cécillon*
- **INRAE URFM :** *Bruno Fady*, William Brunetto, Florence Courdier, Frédéric Jean, Nicolas Mariotte
- **INRAE UEFM:** Marianne Corréard, Jean Thévenet
- **EDYTEM:** *Jérôme Poulenard*, Norine Khedim, Yves Perrette, Erwan Messenger, Emmanuel Malet
- **IMBE:** *Cécile Albert, Lenka Brousset*, Raphaël Gros, Frédéric Guibal, Frédéric Guiter, Frédéric Médail, Eric Meineiri, Alexandre Millon, Pascal Mirleau, Pavon Daniel, Arne Saatkamp, Brigitte Talon
- **SAJF:** *Jean-Gabriel Valay*, Rolland Douzet, Maxime Rome,
- **CEN:** *Samuel Morin*
- **Laboratoire de Géologie de l'ENS:** *Lauric Cécillon*, Laure Soucémarianadin
- **CBN Alpin:** *Bertrand Liénard, Sylvain Abdulhak*, Gilbert Billard, Luc Garraud, Thomas Legland, Baptiste Merhan, Gilles Pache, David Paulin, Thomas Sanz, Jérémie Van Es
- **CBN Med:** *Virgile Noble*, Pauline Bravet, Maëlle Le Berre, Matthias Pires, Julien Ugo
- **PN des Ecrins & RI du Lauvitel:** *Richard Bonet*, Cédric Dentant, Jérôme Forêt, Damien Combrisson
- **PN du Mercantour:** *Nathalie Siefert, Marie-France Leccia, Jérôme Mansons*, Matthieu Kramer, Sebastien Honoré
- **PN de la Vanoise:** *Vincent Augé*, Thierry Delahaye, Franck Parchoux
- **PNR du massif des Bauges:** *Jean-François Lopez*
- **PNR de Chartreuse:** *Laure Belmont*, Jessica Bruggeman
- **PNR du Queyras & RN Ristolas-Mont-Viso:** *Anne Goussot, Alain Block*, Nicolas Tenoux
- **ASTER & RN Sixt-Passy:** *Christian Schwoehrer, Carole Birck*, Jean-José Richard Pomet
- **CREA:** *Anne Delestrade*, Irene Alvarez, Bradley Carlson, Hillary Gerardi, Colin Van Reeth
- **N 2000 Clarée:** Laure Vuinée
- **Natura 2000 Dévoluy-Durbon-Charance-Champsaur & SMIGIBA:** *Eric Hustache*
- **Grenoble-Alpes Métropole:** *Alexandre Mignotte*, Pierre-Eymard Biron

4. ORCHAMP Funding

Each institution involved in the consortium is co-funding the project either through in-kind funding or participation to specific projects.

ANR - Agence Nationale de la Recherche: GlobNets (ANR-16- CE02-0009), Origin-Alps (ANR-16-CE93-004)

ANR 'Investissement d'Avenir': Trajectories (ANR-15-IDEX-02), Montane: (OSUG@2020: ANR-10-LAB-56)

AFB - Agence Française pour la Biodiversité: Sentinelles des Alpes

AURA - Région Auvergne-Rhône-Alpes: CBNA regional convention

LTSER ZAA - Zone Atelier Alpes (CNRS, IRSTEA)

Interreg Alcotra FEDER: PITEM Biodiv'ALP

Other local fundings: Parc National des Ecrins (PNE), Réserve intégrale du Lauvitel, Parc National du Mercantour (PNM), Grenoble Alpes Métropole, Agence de l'eau Rhône-Méditerranée Corse (AERMC), Electricité de France (EDF), Mairie du Dévoluy, Institut de Radioastronomie Millimétrique (IRAM), Communauté de communes de la vallée de Chamonix Mont-Blanc

Appendix S2 |_Description of the soil eDNA data processing

1. Soil eDNA extraction, amplification and sequencing

From soil sub-samples C, we conducted part of the soil eDNA extraction immediately in the field each year. In order to liberate eDNA from clay and silica particles, each sample was shaken for 15 minutes by rotation in a 15 mL saturated phosphate buffer solution (Na_2HPO_4 ; 0.12 M; pH \approx 8). We then sampled and centrifuged 2 mL of sediment/buffer mixture for 10 minutes at 10,000 g. We collected a 400 μL aliquot of supernatant and used it as starting material for eDNA extraction using NucleoSpin® Soil extraction kit (Macherey-Nagel GmbH, Düren, Germany), following manufacturer's instructions except skipping the lysis cell step (Taberlet *et al.* 2012). We stored the samples in a dry environment before the elution step, which we performed back at LECA, Laboratoire d'Ecologie Alpine, France. After elution, soil eDNA extracts were diluted 10 times before being used as templates for amplification. A total 268 negative extraction controls were also performed over the three years to identify potential extraction contaminants.

For eDNA amplification, we targeted Eukaryotes, Fungi and Bacteria using respectively the DNA markers Euka02 (18S rRNA), Fung02 (ITS) and Bact01 (16S rRNA) described in Taberlet *et al.* 2018. We added unique eight-base long tags at the 5' end of each primer so that the sample of origin of each sequencing read can be retrieved after sequencing. These tags modified from Binladen *et al.* 2007 and Valentini *et al.* 2009 differed by at least five bases. DNA amplifications were carried out in a final volume of 20 μL containing i) 2 μL of eDNA sample, ii) 10 μL of AmpliTaq Gold 360 Master Mix 2X (Applied Biosystems™, Foster City, CA, USA), iii) 2 μL of primers mix at initial concentration of 5 μM of each primer and iv) 0.16 μL of Bovine Serum Albumin. We included a total of 184 negative- and 84 positive PCR-controls over the three years to identify potential PCR-contaminants. Four PCR-replicates were amplified for each sample and control.

We performed PCRs as follow: 1) samples and controls were first incubated 10 min at 95°C, 2) they underwent 45 cycles of i) 30 s at 95°C, ii) 30 s at 57°C (Bact01), 55°C (Fung02) or 45°C (Euka02) and iii) 60 s at 72°C, and 3) they went through a final elongation at 72°C for 7 minutes. Then, we 4) checked the amplification success using capillary electrophoresis (QIAxcel System; Qiagen), 5) mixed PCR products in an equi-volume way (15 μl each) and 6) purified 8*100 μL -aliquots of the resulting mix using MinElute Purification kit (Qiagen GmbH, Hilden, Germany). Finally, we pooled purified products together before sequencing.

Sequencing was performed by pair-end sequencing on Illumina HiSeq 2000 platform (2*125 for Euka02, and 2*250 for both Bact01 and Fung02) at Fasteris, Geneva, Switzerland. Data were splitted into 4 libraries for sequencing (2016, 2017 A&B, 2018). We also included 728 negative sequencing controls over the three years to retrieve false positives caused by tag-switching events during the sequencing.

Figure S2-A1: Overview of the cleaning and preparation steps of metabarcoding data from sequences to a MOTUs-sample matrix for each trophic class. Green boxes and arrows correspond to steps done with functions belonging to the OBITools package. Blue boxes and arrows correspond to steps done with functions belonging to metabar package. Yellow and oranges boxes and arrows correspond respectively to assignment to a taxonomical path and a trophic class and trophic group. Arrows on the right lists the function used at each step

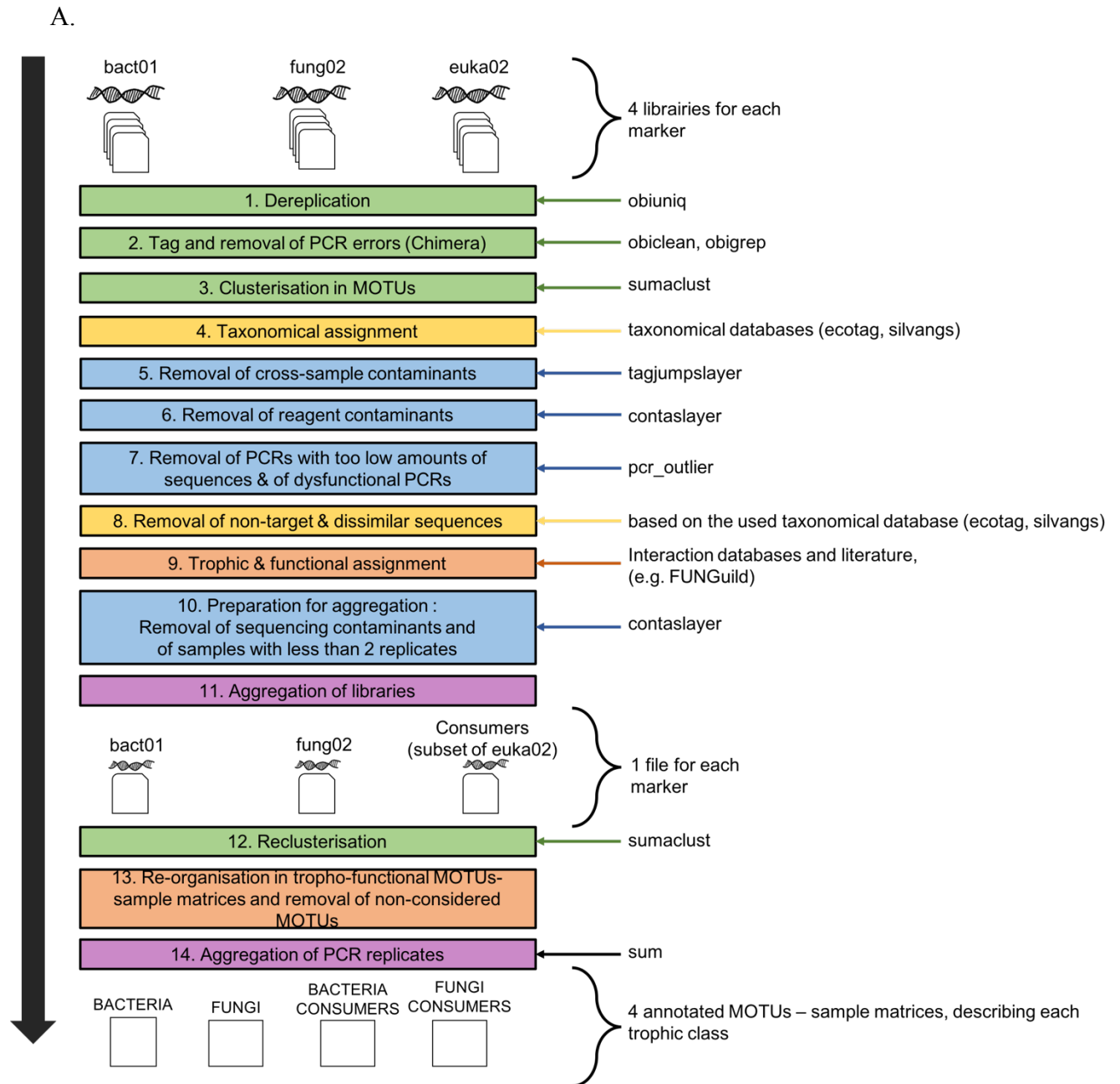


Table S2 – A1: Number of reads and MOTUs for the sample at each cleaning or preparation step, for each marker and each library. Preparation steps and colors correspond to the ones described by Figure S2 – A1.

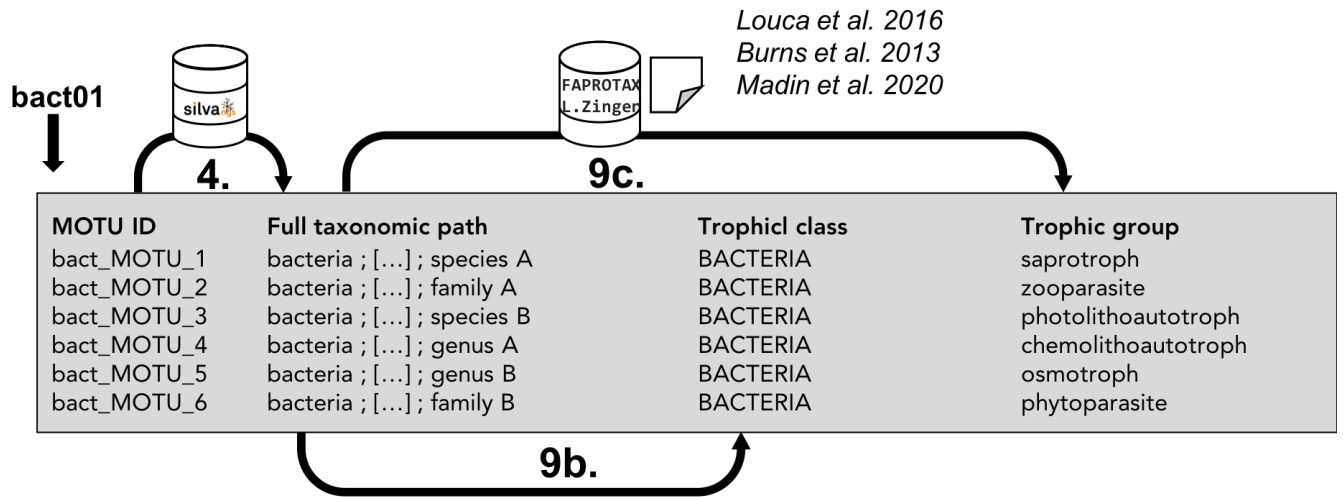
Preparation step	initial marker ->	bact01		fung02		euka02	
	library / year	Nb MOTUs	Nb reads	Nb MOTUs	Nb reads	Nb MOTUs	Nb reads
1.	2016						
	2017 A						
	2017 B						
	2018						
2.	2016						
	2017 A						
	2017 B						
	2018						
3.	2016	65970	4306923	37252	6260060	15613	9922423
	2017 A	56653	4361942	36606	8917303	15388	8840773
	2017 B	55535	3991434	36830	10993612	14300	8373465
	2018	56306	3636825	20546	8432630	12892	5393325
4.	2016	65970	4306923	37252	6260060	15613	9922423
	2017 A	56653	4361942	36606	8917303	15388	8840773
	2017 B	55535	3991434	36830	10993612	14300	8373465
	2018	56306	3636825	20546	8432630	12892	5393325
5.	2016	65948	4277724	37252	6105170	15494	9169312
	2017 A	56498	4253104	36534	8745025	15286	8312455
	2017 B	55462	3966722	36759	10453765	14093	8121633
	2018	56123	3566229	20453	7810381	12809	5257314
6.	2016	65540	4151729	37245	6104984	15377	8852668
	2017 A	55087	3611820	36515	8742015	14610	8092448
	2017 B	53435	3098173	36732	10451475	13004	7496947
	2018	54302	2599510	20431	7808920	12607	3960067
7.	2016	65217	3984826	35538	6007559	15309	8688037
	2017 A	54700	3542538	35834	8711666	14240	7950499
	2017 B	53123	3052218	36514	10448195	12930	7464058
	2018	53574	2538139	20390	7762144	12582	3893344
8.	2016	63327	3976796	7263	4066180	11904	8086712
	2017 A	53513	3539099	10597	6265723	11794	7739560
	2017 B	52165	3049560	11518	7688393	10798	7288180
	2018	53474	2537752	10627	6167321	10469	3686627
9.	2016	63327	3976796	7263	4066180	2666	433512
	2017 A	53513	3539099	10597	6265723	2451	357287
	2017 B	52165	3049560	11518	7688393	2192	237341
	2018	53474	2537752	10627	6167321	2586	318699
10.	2016	63327	3976796	7262	4066179	2664	433510
	2017 A	53513	3539099	10597	6265723	2451	357287
	2017 B	52165	3049560	11515	7688384	2191	237340
	2018	53453	2537711	10624	6167313	2586	318699
11.	all libraries aggregated	175742	12610039	32384	23094281	5761	1272995
12.	all libraries	111680	12610039	20773	23094281	4587	1272995

Table S2 – A2: Number of extraction-, negative PCR-, positive PCR-, and sequencing controls, Number of samples before and after data curation, Number of pcr replicates before and after data curation for each marker and each library.

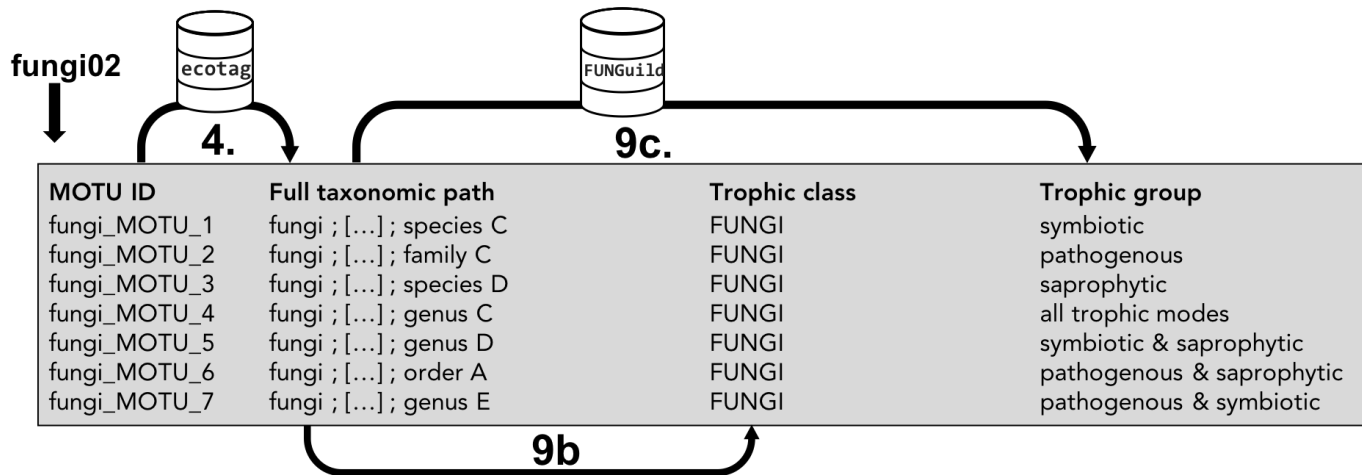
library/year	Nb of extraction controls	Nb of negative PCR controls	Nb of positive PCR controls	Nb of sequencing controls	Nb of samples before data curation	Nb of samples after data curation			Nb of pcr replicates before data curation	Nb of pcr replicates after data		
						bact01	fung02	euka02		bact01	fung02	euka02
2016	40	24	0	392	174	162	166	174	696	519	544	639
2017 A	52	40	24	96	139	136	134	136	556	511	528	499
2017 B	88	44	24	96	129	127	128	128	516	483	509	494
2018	88	76	36	144	202	200	202	200	808	755	794	795

Figure S2-A2: Details of the assignment to a taxonomical path, to a trophic class and to trophic group for the metabarcoding marker A. bact01, B. fungi02, C. euka02. The cylindrical schematics detail the databases used at each step. The paper schematics detail the literature used at each step. Steps are numerated according to Figure S2-A1.

A.



B.



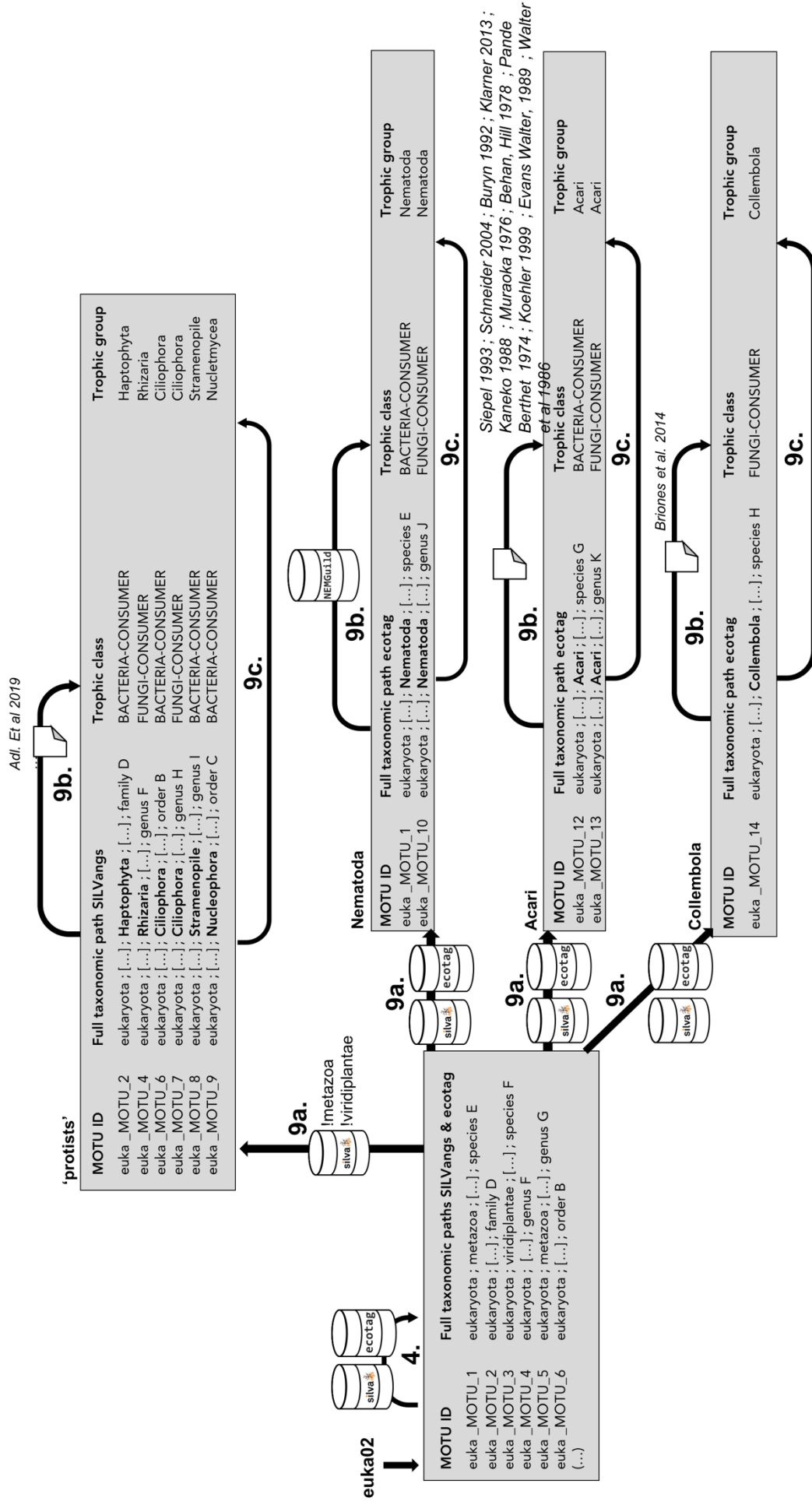
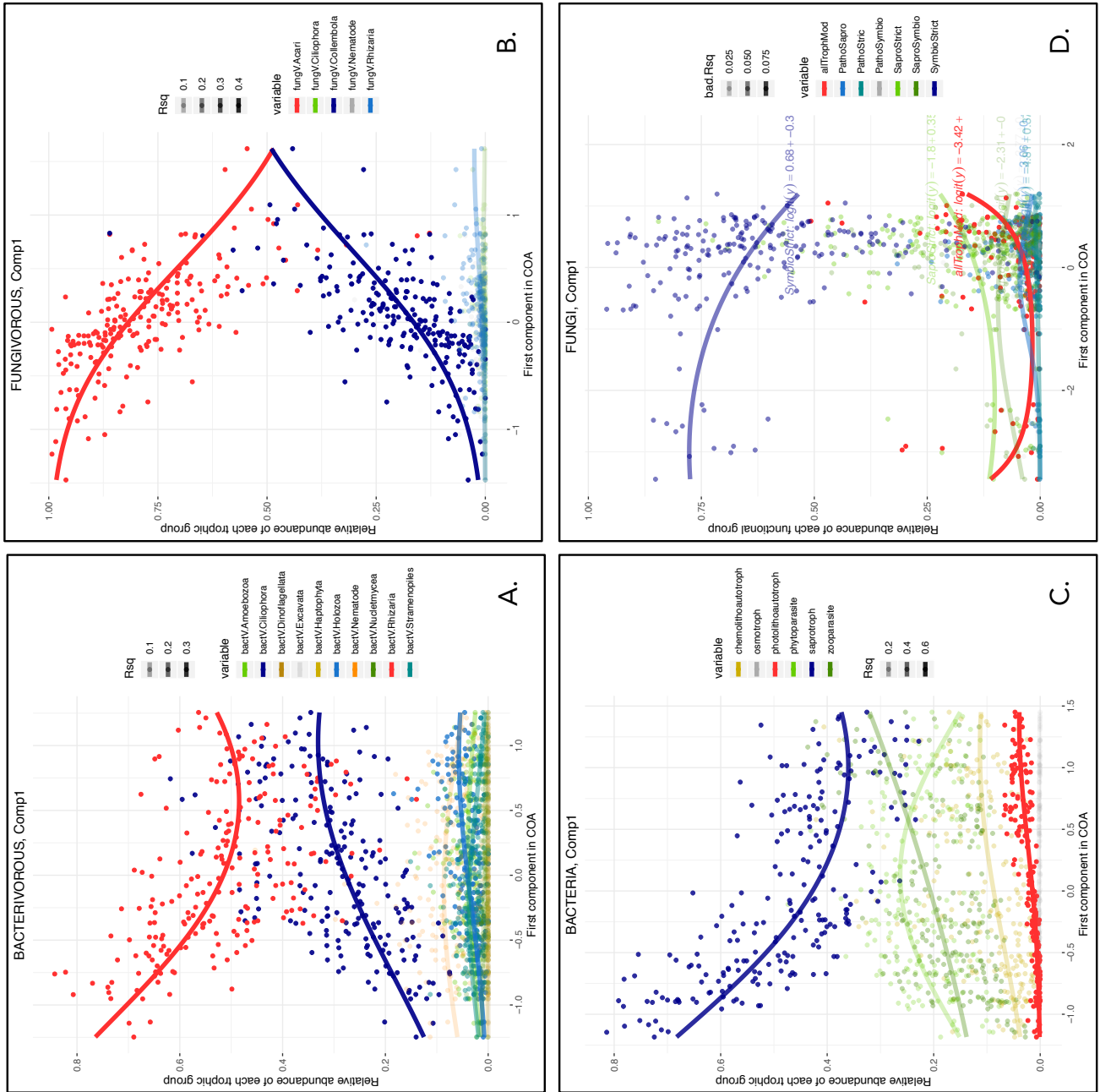


Table S2 – A3: Characteristics of the trophic classes and trophic groups. Total number of MOTUs and reads, average number of MOTUs and reads of trophic classes, number of MOTUs and reads of trophic groups, also expressed as percentage of the corresponding trophic class

Trophic level	Trophic class	Nb motus		Nb reads		Average nb motus by sample (sd)		Average nb reads by sample (sd)		Trophic group	Nb motus (% nb motus trophic class)		Nb reads (% nb reads trophic class)	
		F	O	F	O	F	O	F	O		F	O	F	O
microbiome	bacteria	73457	96783	4498164	7467886	3347.335 (1378.936)	3417.874 (1312.949)	21217.75 (13402.17)	21336.82 (14733.9)	chemolitho-autotroph	2062 (2.8)	2893 (3.0)	103656 (2.3)	183413 (2.5)
										osmotroph	139 (0.19)	215 (0.22)	2216 (0.049)	3902 (0.052)
										photolitho-autotroph	438 (0.60)	781 (0.81)	21733 (0.48)	48745 (0.65)
										phytoparasite	4255 (5.8)	4834 (5.0)	277071 (6.2)	279700 (3.7)
										saprotroph	8147 (11)	9959 (10)	575920 (13)	928379 (12)
										zooparasite	3301 (4.5)	3807 (3.9)	267092 (5.9)	300108 (4.0)
										unknown	55115 (75)	74294 (77)	3250476 (72)	5723639 (77)
	fungi	11857	13734	8934394	13400912	319.5189 (120.3817)	312.2543 (142.2961)	42143.37 (22750.61)	38288.32 (22575.02)	all functions	842 (7.1)	999 (7.3)	412829 (4.6)	551529 (4.1)
										pathogenic & saprophytic	557 (4.7)	760 (5.5)	288577 (3.2)	641911 (4.8)
										pathogenic & symbiotic	209 (1.8)	117 (0.85)	182033 (2.0)	100575 (0.75)
										pathogenic strict	387 (3.3)	447 (3.3)	66837 (0.75)	150531 (1.1)
										saprophytic & symbiotic	737 (6.2)	1172 (8.5)	688327 (7.7)	2881851 (22)
										saprophytic strict	2345 (20)	3175 (23)	1264641 (14)	3310091 (25)
										symbiotic stric	3807 (32)	3179 (23)	5360927 (60)	4019694 (30)
unknown	2973 (25)	3885 (28)	670223 (7.5)	1744730 (13)										
consumers	bacteria-consumers	2377	3181	135739	383524	133.4858 (71.2693)	153.7486 (63.38372)	640.2783 (662.5135)	1095.783 (1031.628)	Nematoda	90 (3.8)	121 (3.8)	10356 (7.6)	48393 (13)
										Ciliophora	610 (26)	797 (25)	35384 (26)	128354 (33)
										Stramenopiles	90 (3.8)	119 (3.7)	3805 (2.8)	7357 (1.9)
										Amoebozoa	291 (12)	410 (13)	4448 (3.3)	10824 (2.8)
										Dinoflagellata	4 (0.17)	2 (0.063)	18 (0.013)	28 (0.0073)
										Excavata	7 (0.29)	7 (0.22)	22 (0.016)	25 (0.0065)
										Haptophyta	20 (0.84)	24 (0.75)	280 (0.21)	851 (0.22)
										Holozoa	167 (7.0)	200 (6.3)	5007 (3.7)	10128 (2.64)
										Nuclletmycea	47 (2.0)	56 (1.8)	1035 (0.76)	1419 (0.37)
	Rhizaria	1051 (44)	1445 (45)	75384 (56)	176145 (46)									
	fungi-consumers	561	676	388549	270766	31.16981 (11.43659)	24.01429 (10.28601)	1832.778 (1658.171)	773.6171 (791.7108)	Acari	194 (35)	204 (30)	313514 (81)	192510 (71)
										Collembola	192 (34)	220 (33)	68134 (18)	65567 (24)
										Nematoda	42 (7.5)	60 (8.9)	2396 (0.62)	2543 (0.94)
										Ciliophora	9 (1.6)	14 (2.1)	1170 (0.30)	3072 (1.1)
Rhizaria										124 (22)	178 (26)	3335 (0.86)	7074 (2.6)	

Figure S3-A1. Compositional change between samples in forests, for A. bacteria-consumers, B. Fungi-consumers, C. Bacteria, D. Fungi. This supplementary figure corresponds to the panels A, B, C & D of the main figure 1, which were simplified for the sake of readability.

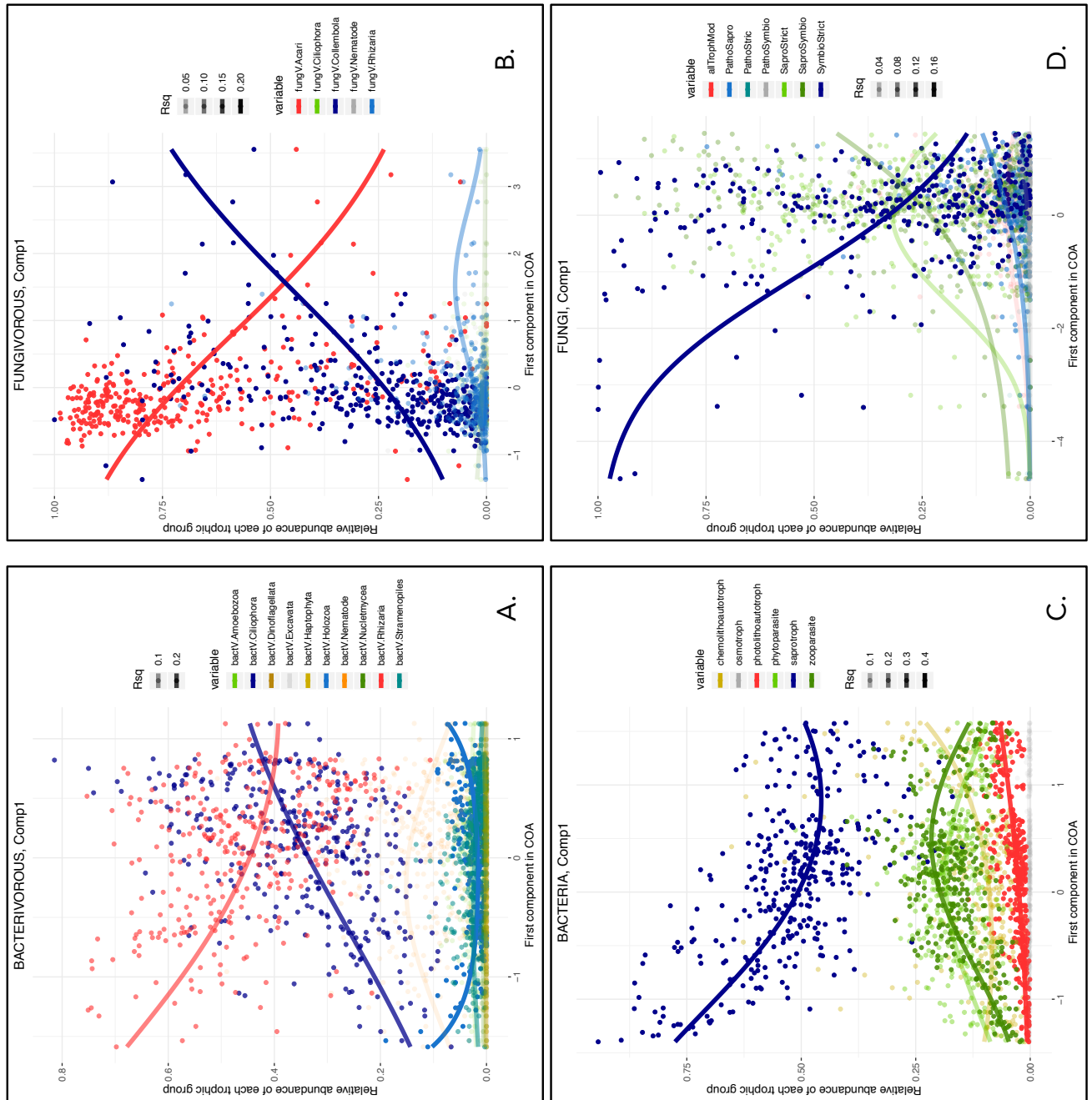


FORESTS

Consumers

Microbiome

Figure S3-A2. Compositional change between samples in open-habitats, for A. bacteria-consumers, B. Fungi-consumers, C. Bacteria, D. Fungi. This supplementary figure corresponds to the panels A, B, C&D of the main figure 2, which were simplified for the sake of readability.



OPEN-HABITATS

Consumers

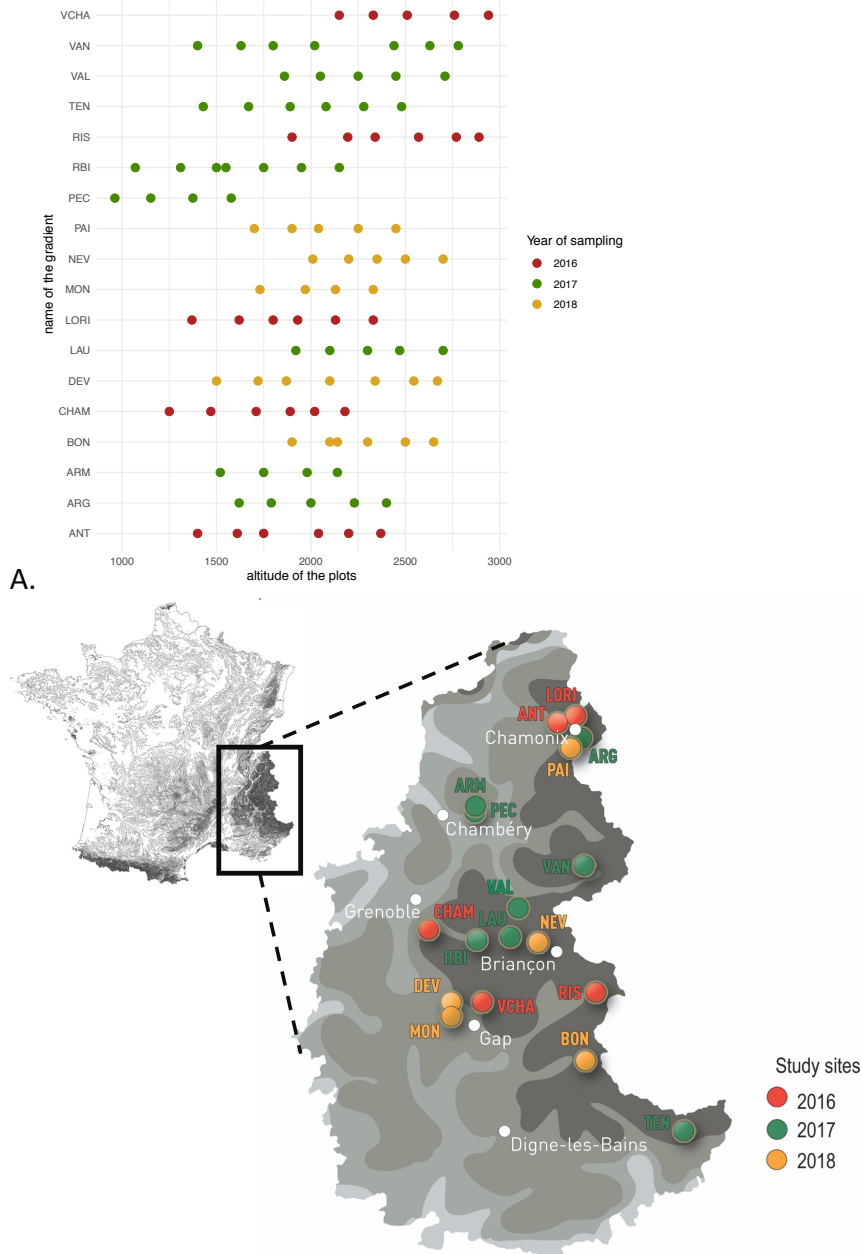
Microbiome

3. Annexes du chapitre 3

Supplementary material Appendix 1 | ORCHAMP: Spatio-temporal observatory of biodiversity and ecosystem functioning of mountains' socio-ecosystems

1. Brief description

Voir Annexes chapitre 2, Appendix S1.



B.

Figure A1: Overview of the 18 gradients of ORCHAMP used in this study: Repartition of the elevations per gradient (A), location of gradients (B), names and year of sampling (A, B).

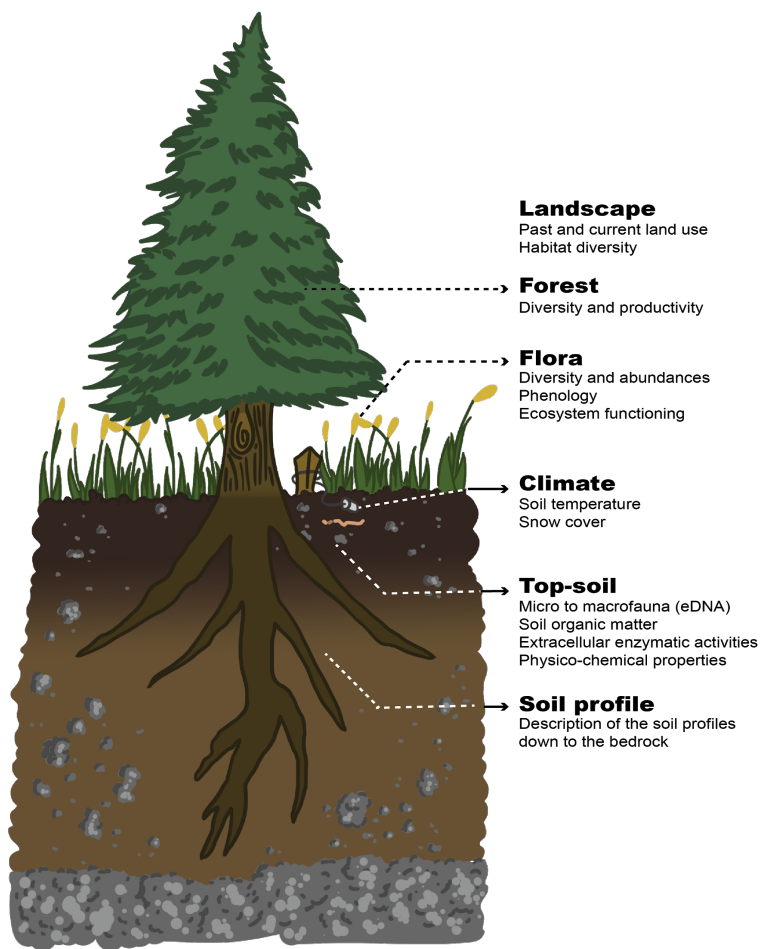


Figure A2: Overview of all measures of landscape, pedo-climatic environment and biodiversity taken on each plot of ORCHAMP

2. Institutions involved in ORCHAMP

Voir les annexes du Chapitre 2, Appendix S1.

3. ORCHAMP Consortium (contact persons are in italics)

Voir les annexes du Chapitre 2, Appendix S1.

4. ORCHAMP Funding

Voir les annexes du Chapitre 2, Appendix S1.

Supplementary material Appendix 2

Table A1: Overview of modelled species, their full names, their average trait values and the total number of occurrences in the 99 plots. *Species abbr.* correspond to the abbreviations used in the paper. *Taxref* corresponds to the French National taxonomic repository (<https://inpn.mnhn.fr/programme/referentiel-taxonomique-taxref>). Traits were retrieved from our own trait database, and averaged at the species level. On average 10 individuals were sampled over different environmental conditions typical for the French Alps following standard protocols. For some species we had to adapt this strategy: We approximated *Cerastium arvense* subsp. *strictum* leaf carbon and nitrogen contents with leaf carbon and nitrogen from *Cerastium arvense* subsp. *suffruticosum*. We retrieved LDMC and SLA for *Melampyrum sylvaticum* and for *Potentilla crantzii* from TRY (www.try-db.org).

Species full names	Species abbr.	Taxref	Leaf Dry Matter Content (mg.g ⁻¹)	Plant Height (cm)	Specific Leaf Area (m.kg ⁻¹)	Leaf C/N	Nb of occurrences
<i>Antennaria dioica</i> (L.) Gaertn.	A. dio	82796	277.44	14	14.3	34.52	28
<i>Anthoxanthum odoratum</i> L.	A. odo	82922	282.05	27.5	29.42	19.89	63
<i>Arnica montana</i> L.	A. mon	83874	162.53	30	20.28	24.67	26
<i>Avenella flexuosa</i> (L.) Drejer	A. fle	85418	307.82	45	3.63	16.63	48
<i>Bistorta vivipara</i> (L.) Delarbre	B. viv	86082	244.67	18.75	15.34	17.49	30
<i>Botrychium lunaria</i> (L.) Sw.	B. lun	86183	193.64	15.67	23.12	9.86	30
<i>Campanula rhomboidalis</i> L.	C. rho	87716	226.31	45	28.74	17.1	21
<i>Chaerophyllum villarsii</i> W. D. J. Koch	C. vil	90359	163.55	75	48.83	11.55	23
<i>Euphrasia minima</i> DC.	E. min	97772	187.84	4	15.75	31.8	30
<i>Festuca laevigata</i> Gaudin	F. lae	98319	314.07	40	8.14	33.91	33
<i>Festuca nigrescens</i> Lam.	F. nig	98404	302.97	45	8.27	31.07	23
<i>Festuca violacea</i> Gaudin	F. vio	98607	356.11	30	6.47	21.8	28
<i>Galium pumilum</i> Murray	G. pum	99511	185.24	25	18.9	19.18	31
<i>Gentiana acaulis</i> L.	G. aca	99854	221.69	9.5	17.53	19.93	23
<i>Geranium sylvaticum</i> L.	G. syl	100160	251.09	50	20.52	21.3	22
<i>Geum montanum</i> L.	G. mon	100208	282.83	10	13.03	33.15	36
<i>Helianthemum nummularium</i> (L.) Mill.	H. num	100956	239.81	16.25	17.32	14.26	24
<i>Homogyne alpina</i> (L.) Cass.	H. alp	102925	235.71	15	11.97	24.46	41
<i>Leontodon hispidus</i> L.	L. his	105502	152.42	27.5	25.93	20.99	29

<i>Melampyrum sylvaticum</i> L.	M. syl	107800	156.15	20	41.4	28.71	23
<i>Myosotis alpestris</i> F. W. Schmidt	M. alp	108987	167.51	11.75	42.5	14.1	26
<i>Nardus stricta</i> L.	N. str	109366	370.62	18.5	5.56	23.75	43
<i>Phleum rhaeticum</i> (Humphries) Rauschert	P. rha	113224	261.81	30	31.74	18.59	23
<i>Phyteuma betonicifolium</i> Vill.	P. bet	113361	218.44	50	30.03	12.03	20
<i>Picea abies</i> (L.) H. Karst.	P. abi	113432	534.81	2500	2.71	39.52	25
<i>Plantago alpina</i> L.	Pl. alp	113806	199.62	7	12.83	22.2	37
<i>Poa alpina</i> L.	P. alp	114105	286.4	23.33	18.98	26.92	39
<i>Potentilla aurea</i> L.	P. aur	115414	283.6	15	20.56	17.01	36
<i>Potentilla crantzii</i> (Crantz) Fritsch	P. cra	115449	327.26	13.33	15.22	17.96	21
<i>Potentilla grandiflora</i> L.	P. gra	115498	327.21	22.5	14.53	19.33	33
<i>Sesleria caerulea</i> (L.) Ard.	S. cae	123071	325.89	27.5	19.37	27.53	23
<i>Soldanella alpina</i> L.	S. alp	124139	242.22	9	12.22	25.71	23
<i>Thymus pulegioides</i> L.	T. pul	126566	314.33	11.83	14.67	20.99	23
<i>Trifolium alpinum</i> L.	T. alp	127219	294.34	11.25	22.22	15.87	24
<i>Trifolium pratense</i> L.	T. pra	127439	230.78	25.67	28.62	13.52	21
<i>Vaccinium myrtillus</i> L.	V. myr	128345	312.1	27.5	19.96	28.87	53
<i>Vaccinium vitis-idaea</i> L.	V. vit	128355	374.12	12	9.91	55.9	22
<i>Viola calcarata</i> L.	V. cal	129527	185.19	9.25	22.54	19.99	37
<i>Campanula scheuchzeri</i> Vill.	C. sch	132522	269.26	20	16.15	20.1	54
<i>Carex sempervirens</i> Vill.	C. sem	132810	347.93	30	13.6	30.53	51
<i>Cerastium arvense</i> L.	C. arv	133087	212.58	10	22.06	22.39	39
<i>Juniperus communis</i> L.	J. com	136974	500.95	40	1.96	51.02	25
<i>Lotus corniculatus</i> L.	L. cor	137438	202.18	5	17.83	10.11	37
<i>Scorzoneroides pyrenaica</i> (Gouan) Holub	S. pyr	612627	174.32	12	22.14	23.8	23

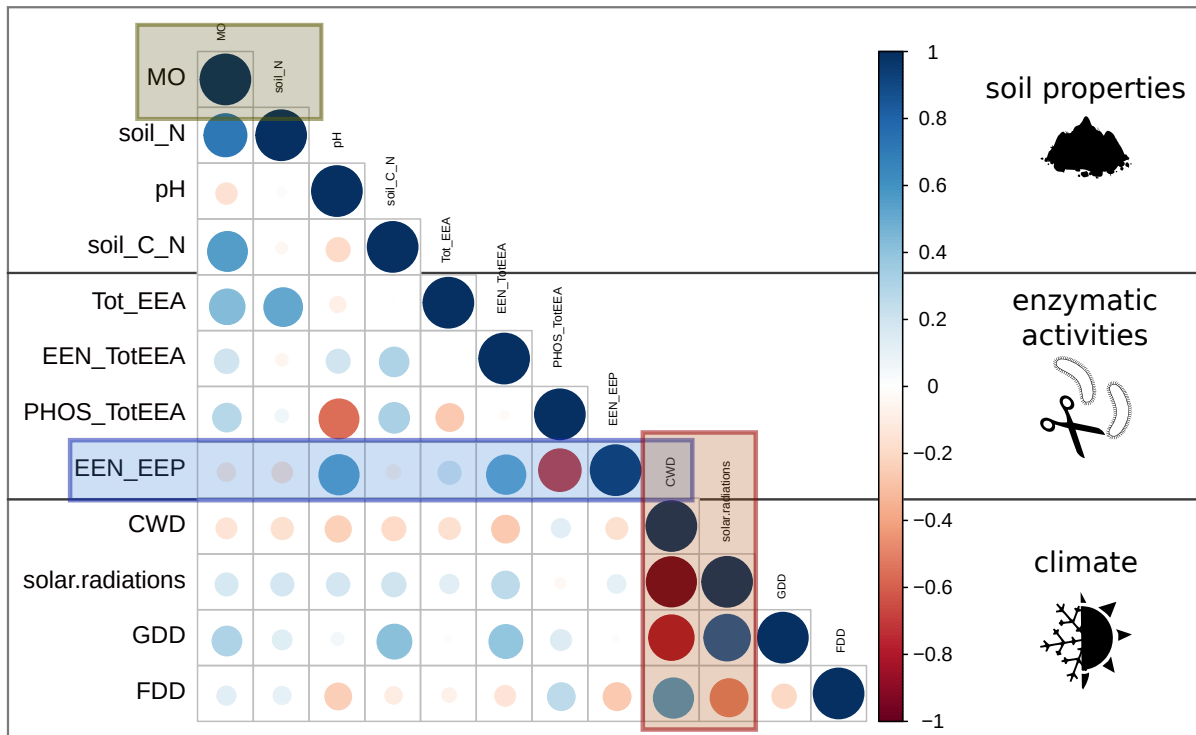


Figure A3: Pairwise correlations between environmental variables. We used the findCorrelation of the package caret in R to identify which variables to remove to reduce pairwise correlations below 0,6 (Kuhn 2008). The selection was in line with our understanding of the variable importance for plant distributions, given the data and the literature. Indeed, one variable characterizing soil properties, soil organic matter (MO, highlighted by the kaki box), one variable characterizing enzymatic activities, the ratio of enzymatic activities targeting nitrogen and phosphorous (EEN/EEP, highlighted by the blue box) and two variables characterizing climate, climatic water deficit and solar radiations (respectively CWD & solar.radiations, highlighted by the red box) were removed, which conserved the balance between the three categories of predictors. Moreover, among variables characterizing soil properties, MO was only a weak predictor of alpine plant distributions in the literature (Vonlanthen *et al.* 2006, Dubuis *et al.* 2013, Buri *et al.* 2017, 2020). Among variables characterizing enzymatic activities, we expected EEN/EEP to be associated with plant distributions through an indirect mechanism (see Introduction). Among the variables characterizing climate, although solar radiation was theoretically crucial for plant growth (Körner 2003), it was rarely reported as a significant driver of their distributions (Vonlanthen *et al.* 2006, Choler 2018). Besides, although water availability is crucial for plant distributions, we approximated it in this paper through CWD, which we calculated from air temperature and which we could not measure in situ. Therefore, it seems reasonable to drop solar radiation and CWD in favor to simpler climatic variables as GDD and FDD as advised by Choler (2018).

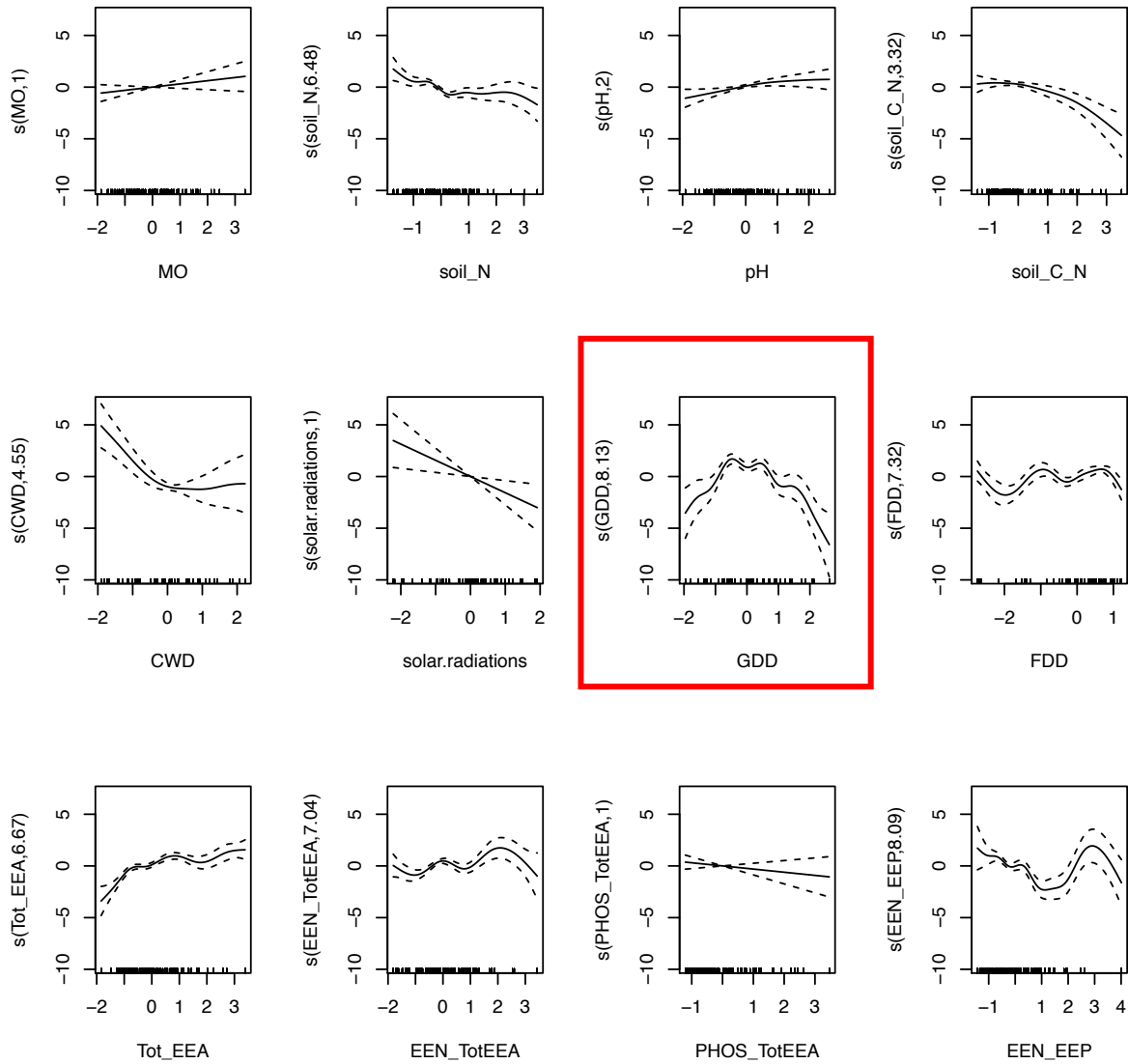


Figure A4: Partial response curves of the selected 44 species to all environmental variables from a generalized additive mixed-effect model. From this, we visually determined that only GDD needed to be modelled with a quadratic term, which is highlighted with a red frame.

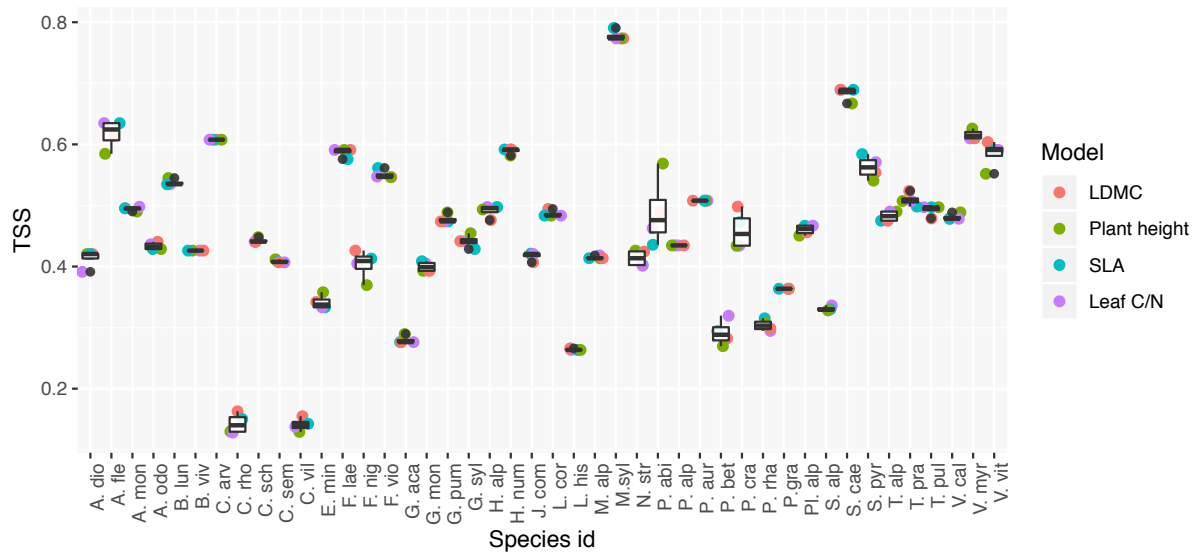


Figure A5: Predictive ability of the hierarchical trait-based species distribution models (independently done for the four traits) as measured by the true skill statistics (TSS). The box corresponds to the median and quartiles across the four models and each colored point corresponds to the TSS value for each trait-specific model.

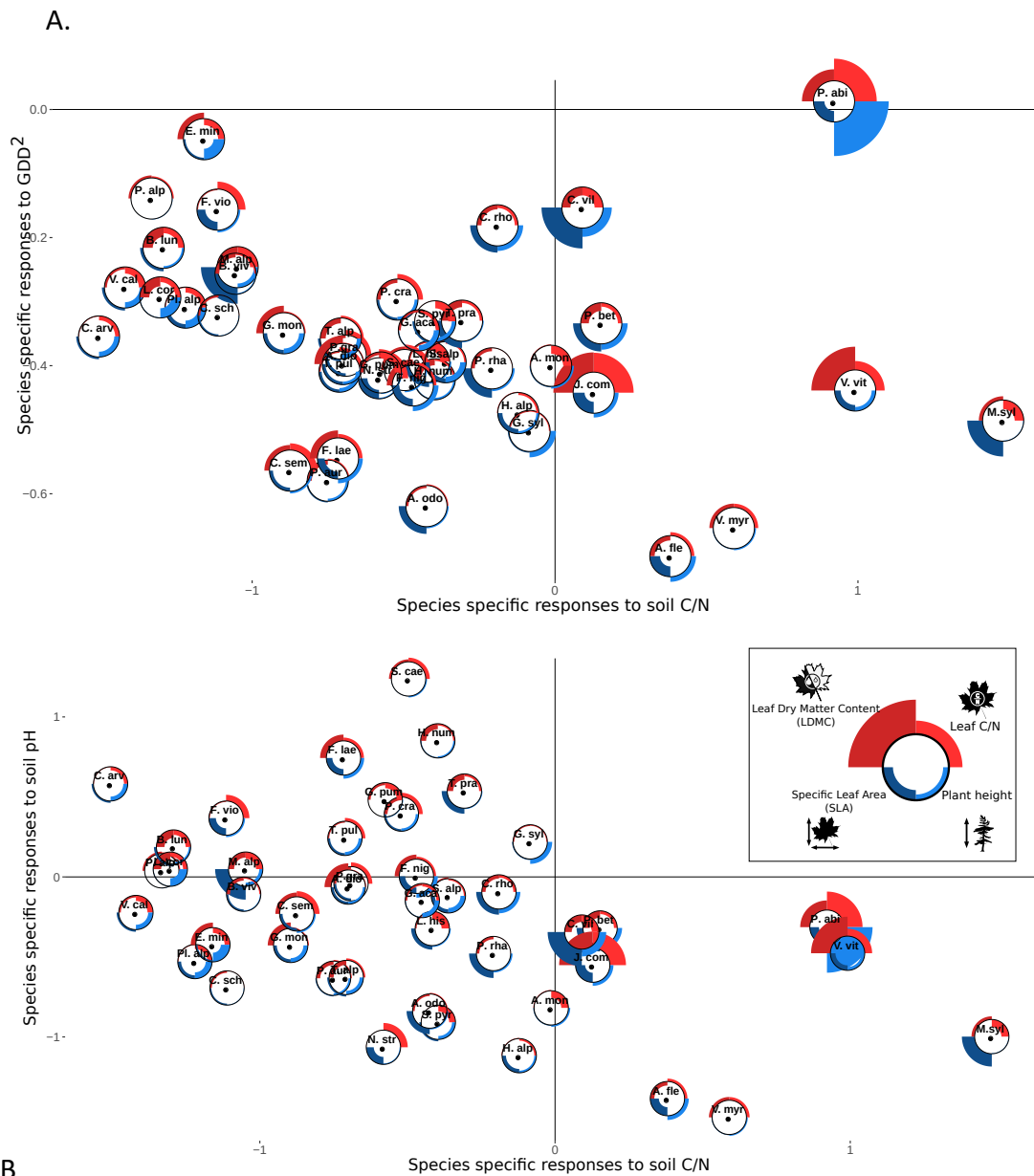


Figure A6: Species-specific partial responses to pairs of environmental gradients, represented by a dot per species. A. GDD² plotted against soil C/N. B. pH plotted against soil C/N. Each functional trait of each species is represented by a quarter of a pie-chart centered on the species dot (SLA: dark blue; plant height: light blue; leaf dry matter content: dark red; leaf C/N: light red, as represented with the example of *Vaccinium vitis-idaea* on the right-up box). For each trait, the dark circle of the pie-charts represents the average of the trait in the dataset. For a given species and a given trait, the colored quarter being within or outside the circle means that this trait value of the species is respectively below or above the dataset average for this trait. Full species names are given in Supplementary material Appendix 2 Table A1.

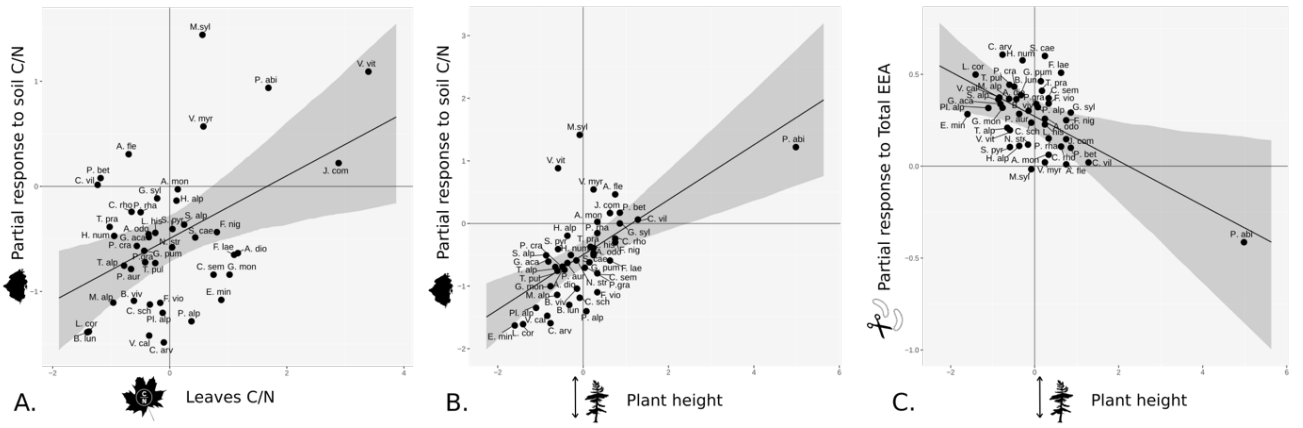


Figure A7: Species partial responses to environmental variables as a function of their functional traits. A. Soil C/N plotted against leaf C/N (model 4); B. Soil C/N plotted against plant height (model 2), C. Total enzymatic activity plotted against plant height (model 3).

4. Annexes du chapitre 4

Materials and Methods

1. ORCHAMP

Voir les annexes du chapitre 2, Appendix 1 pour une brève description, la liste des partenaires, la description du consortium ORCHAMP et les sources de financements.

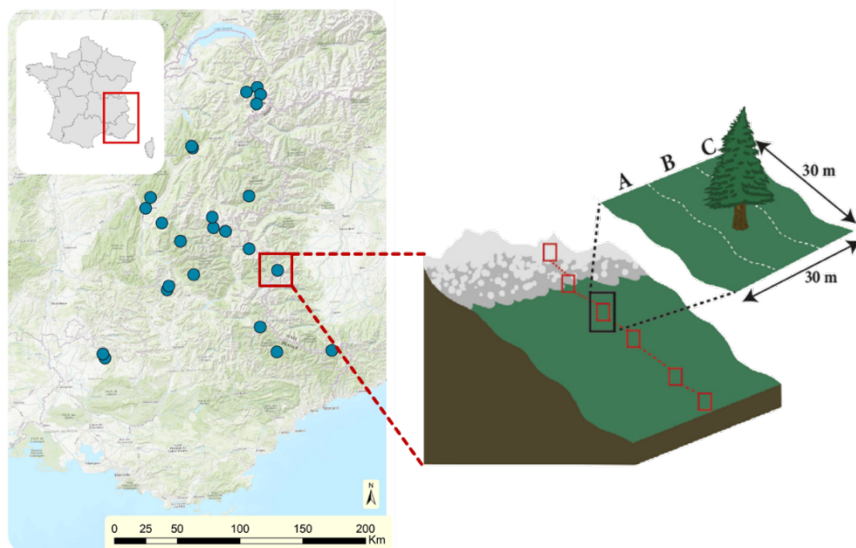


Figure S1: Location and structure of observation network ORCHAMP.

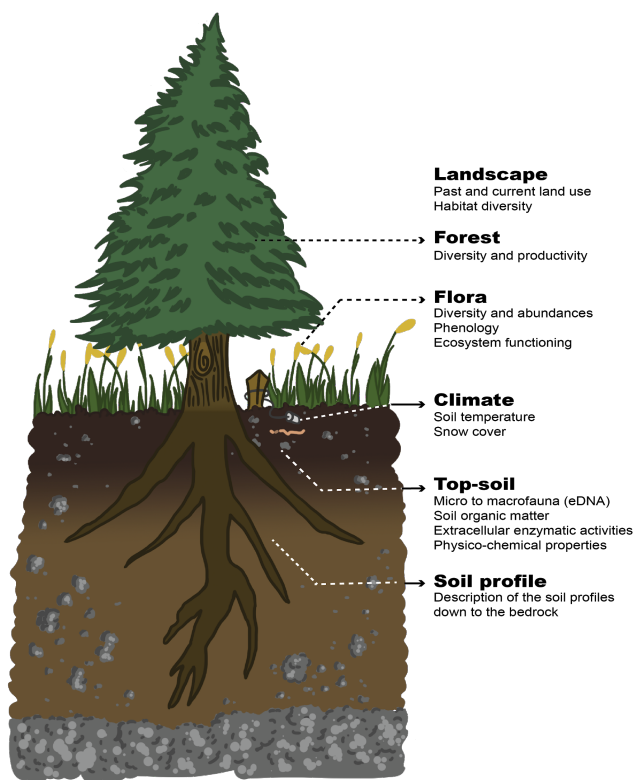


Figure S2: Data that are collected on ORCHAMP plots.

2. Calculating functional richness

Since FRic and species richness are correlated (Villéger *et al.* 2008), we used a randomisation process to calculate the expected FRic value at a given species richness. For every level of species richness i that was observed in the entirety of the plots, a random presence/absence list of i species present in the observation network was created. Then, a theoretical FRic value was calculated using the (transformed and standardized) traits of the randomly selected species. These steps were repeated 900 times for every level of species richness. The standard-effect-size FRic_{ses} for every level of species richness was obtained following Eq. S1:

$$(S1) \quad FRic_{ses} = \frac{FRic_{observed} - \mu(FRic_{theoretical})}{\sigma(FRic_{theoretical})}$$

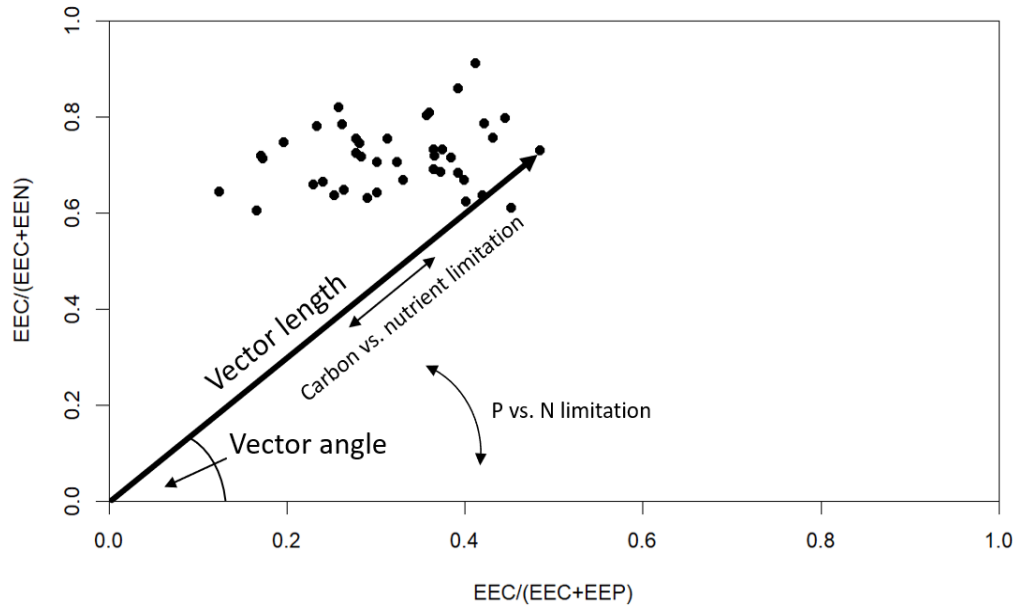
where μ is the mean of all 900 calculated theoretical FRic values at a given level of species richness and σ the standard deviation of the same values.

3. Measuring potential enzymatic activities

The potential activity of α -Glucosidase (AG), β -Glucosidase (BG), β -D-cellubiosidase (CB), β -Xylosidase (XYL), Leucine aminopeptidase (LAP), N-acetyl- β -Glucosaminidase (NAG) and Phosphatase (PHOS), was measured according to an adapted protocol of Bell *et al.* (2013) as follows: Sodium acetate buffer adjusted to the mean pH across sites (pH 5) was used. 2.75g of soil were homogenized in 200mL of buffer using a Waring blender (1min). Then, for each soil sample and each enzyme, 800 μ L of soil slurry were mixed with 200 μ L of substrates at the saturation concentration (established in previous assays) in technical duplicates in 96-deep well microplates. Duplicated standard curves (0-100 μ M concentration) were prepared for each sample by mixing 800 μ L of soil slurry with 200 μ L of 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (MUC) in 96-deep well microplates. The prepared samples were incubated for 3h on a rotary shaker (150rpm) at 20°C followed by a centrifugation at 2900g (3min). The supernatant (250 μ L) was transferred in black Greiner flat-bottomed plates and fluorescence intensity was measured using a VarioSkan Flash 3001-1160 with excitation wavelength set to 365nm and emission set to 450nm. Negative controls were also conducted and used to correct for potential natural degradation of substrate or contamination. Potential enzyme activities were calculated as nmol*g dry soil⁻¹*h⁻¹.

4. Enzymatic stoichiometry

To calculate enzyme activity vectors quantifying the relative investment of the belowground community in C, N and P acquisition according to Moorhead *et al.* (2016), we first plotted the



proportional activity of enzymes targeting carbon (AG, BG, CB and XYL) and nitrogen (LAP and NAG) - i.e. $(AG+BG+CB+XYL)/[(AG+BG+CB+XYL) + (LAP+NAG)]$, in short: $EEC/(EEC+EEN)$ - against C vs. P acquiring enzymes (PHOS) - i.e. $(AG+BG+CB+XYL)/[(AG+BG+CB+XYL) + (PHOS)]$, in short $EEC/(EEC+EEP)$ (Fig. S3).

The length of the vector created by each point in the plot and the origin quantifies relative C vs. nutrient limitation and the angle formed by the x-axis and the vector quantifies the relative P vs. N limitation. Vector length is calculated according to Eq. 1. and Vector angle according to Eq. 2.

$$(1) \quad \text{Vector length} = \sqrt{[EEC/(EEC+EEN)]^2 + [EEC/(EEC+EEP)]^2}$$

$$(2) \quad \text{Vector angle} = \arctan[(EEC/(EEC+EEN)) / (EEC/(EEC+EEP))] * 180/\pi$$

Figure S3: Proportional activity of C vs. N targeting enzymes ($EEC/(EEC+EEN)$) against the proportional activity of C vs. P targeting enzymes ($EEC/(EEC+EEP)$). Vector length is a measure of C vs. nutrient limitation and Vector angle is a measure of P vs. N limitation.

Moorhead *et al.* (2016) used proportional activities instead of ratios (i.e. $EEC/(EEC+EEN)$ instead of EEC/EEN) because they are confined to the interval $[0,1]$, with 1 representing maximal carbon acquisition effort and 0 maximal nutrient acquisition effort (increasing activity targeting a specific element indicating limitation of that element in the environment (Olander & Vitousek 2000)). Therefore, Vector length assumes the value $\sqrt{2}$ at most, eliminating the possibility of infinite values and facilitating interpretation. Similarly, using the variable Vector angle simplifies interpretation of P vs. N limitation: a low angle (generally $< 45^\circ$) indicates a habitat which is more N than P limited since $EEC/(EEC+EEN)$ will be smaller than $EEC/(EEC+EEP)$, therefore EEN must be greater than EEP, and inversely, the habitat will be more P limited the greater the angle.

Network including functional diversity indices

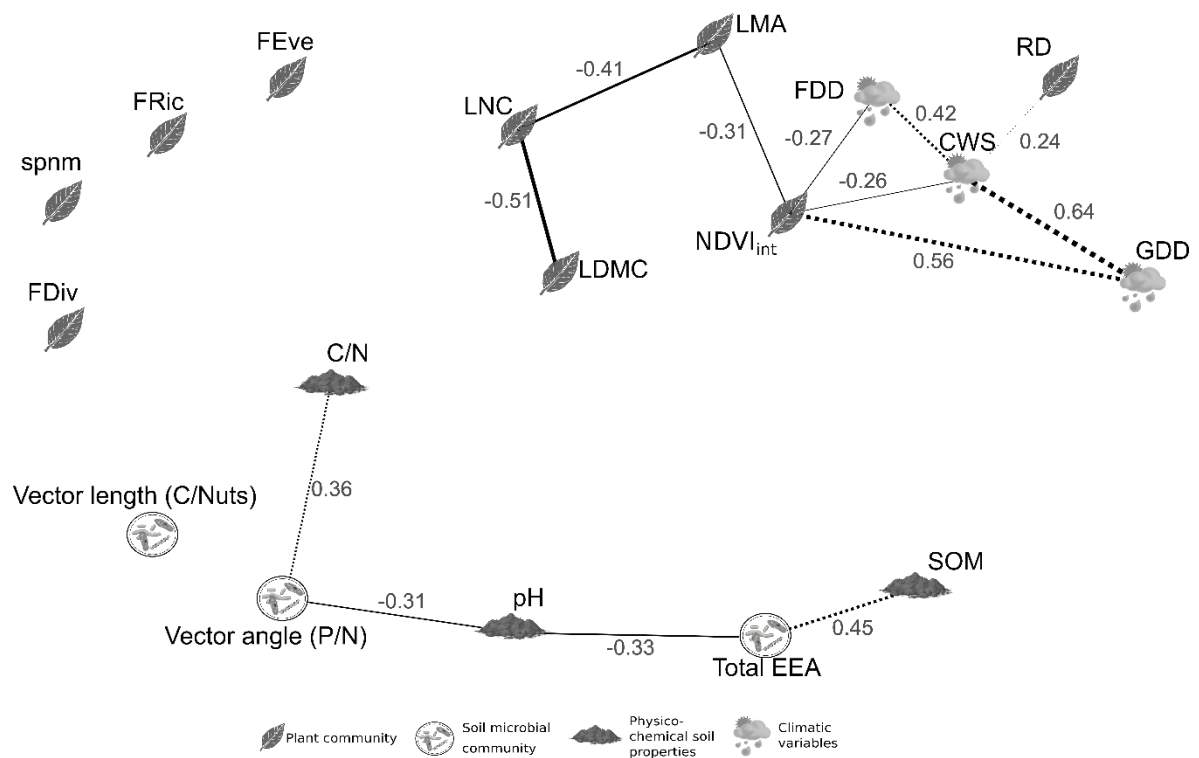


Figure S4: The first partial correlations network inferred with the graphical lasso included all variables. Nodes belong to the groups of the plant community (community weighted means and functional diversity indices), the soil microbial community (represented by enzymatic activities), climatic variables and physico-chemical soil properties. The edge thickness corresponds to the absolute strength of partial correlations. Positive partial correlations are indicated by dotted lines and negative correlations by continuous ones.

Regression on partial correlations to test robustness of results

To test the robustness of the resulting partial correlation network, a regression was carried out on the partial correlations that were present in both the network containing all variables and the network containing the selection of variables.

Altogether, the obtained results seem to be relatively robust because there is a significant correlation between both sets of partial correlations. A linear regression of partial correlations inferred in the last network against partial correlations inferred in the first network gave an R^2 of 0.96, p -value < 0.001 .

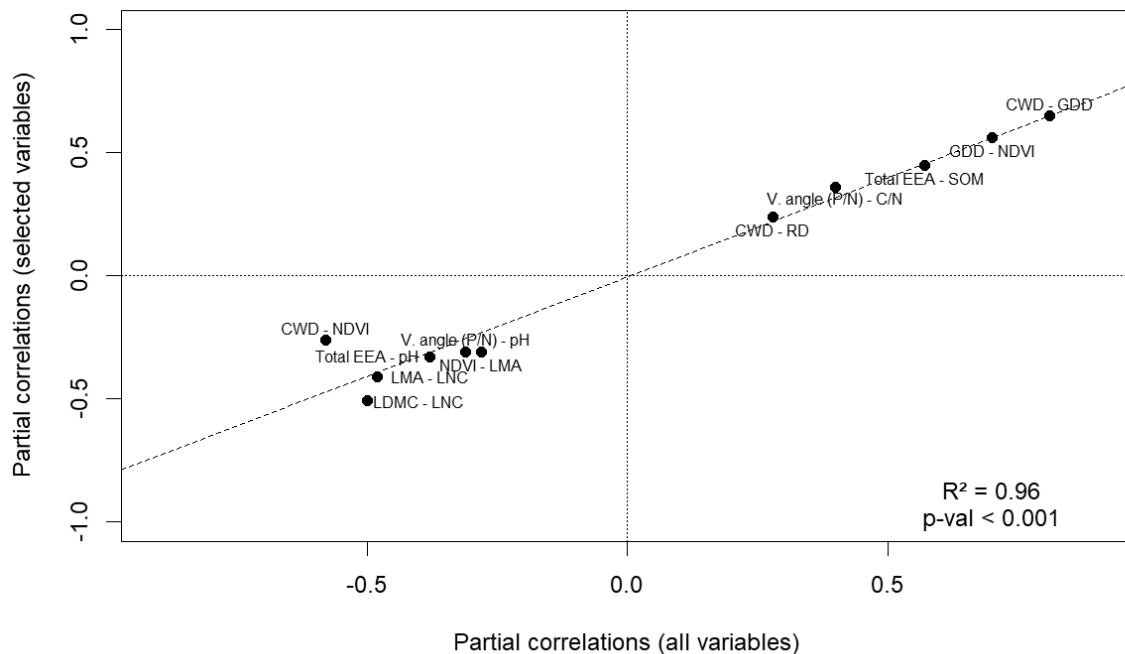


Figure S5: Linear regression of partial correlations that were present in both the first network (including all variables) and the network based on a selection of variables.

Correlation between modelled and real temperatures

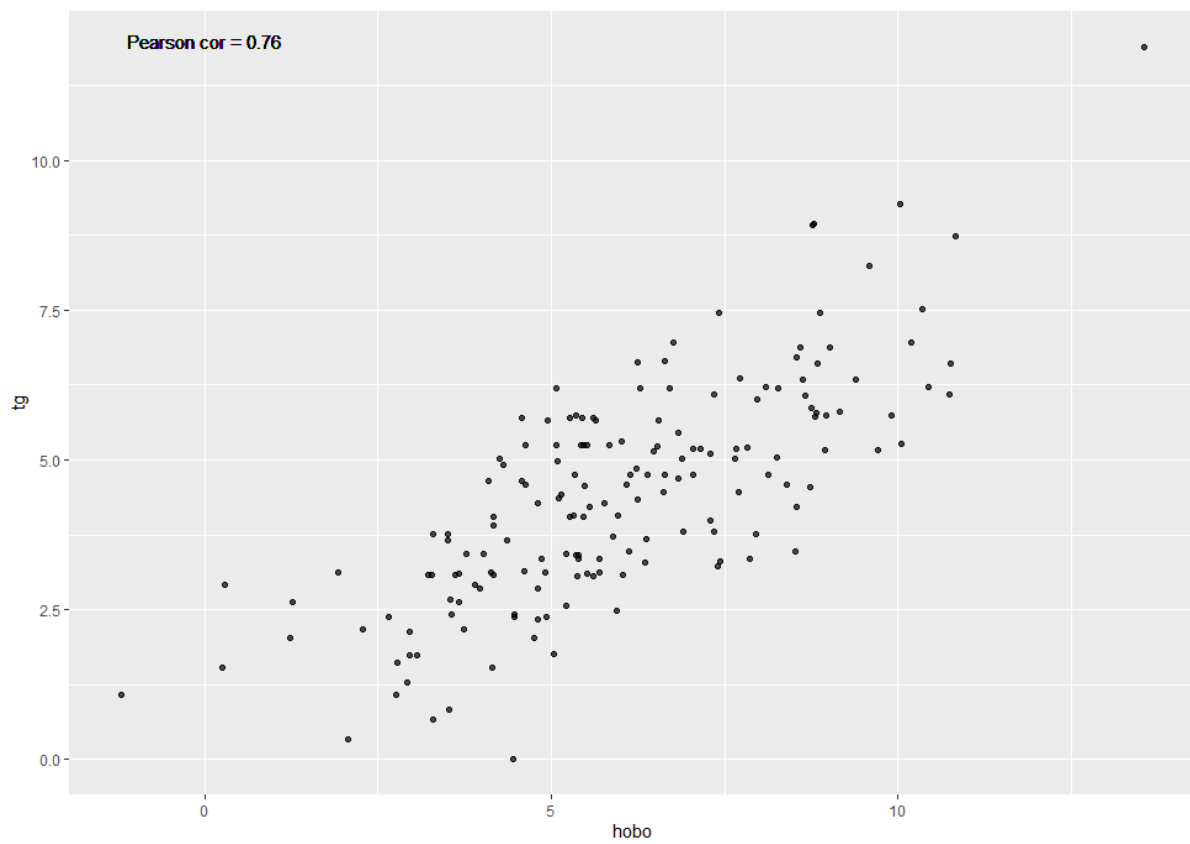


Figure S6: Relationship between the annual mean temperature from the climatic model (y-axis) and the annual mean temperature from the data loggers on Orchamp sites (x-axis).

Correlation between growing degree days calculated over different time periods

Plants and their traits respond to long-term climate while soil activities might be more prone to short-term variations of climatic conditions. However, it has been suggested that soil organisms might also be the organisms with the largest climatic tolerance (Takhur 2020), which may therefore reconcile these scale mismatches. To determine whether this temporal mismatch was truly an issue, we compared GDD calculated for a 30-year time period with GDD calculated over 10 years and over the year before sampling (Fig. S7, S8).

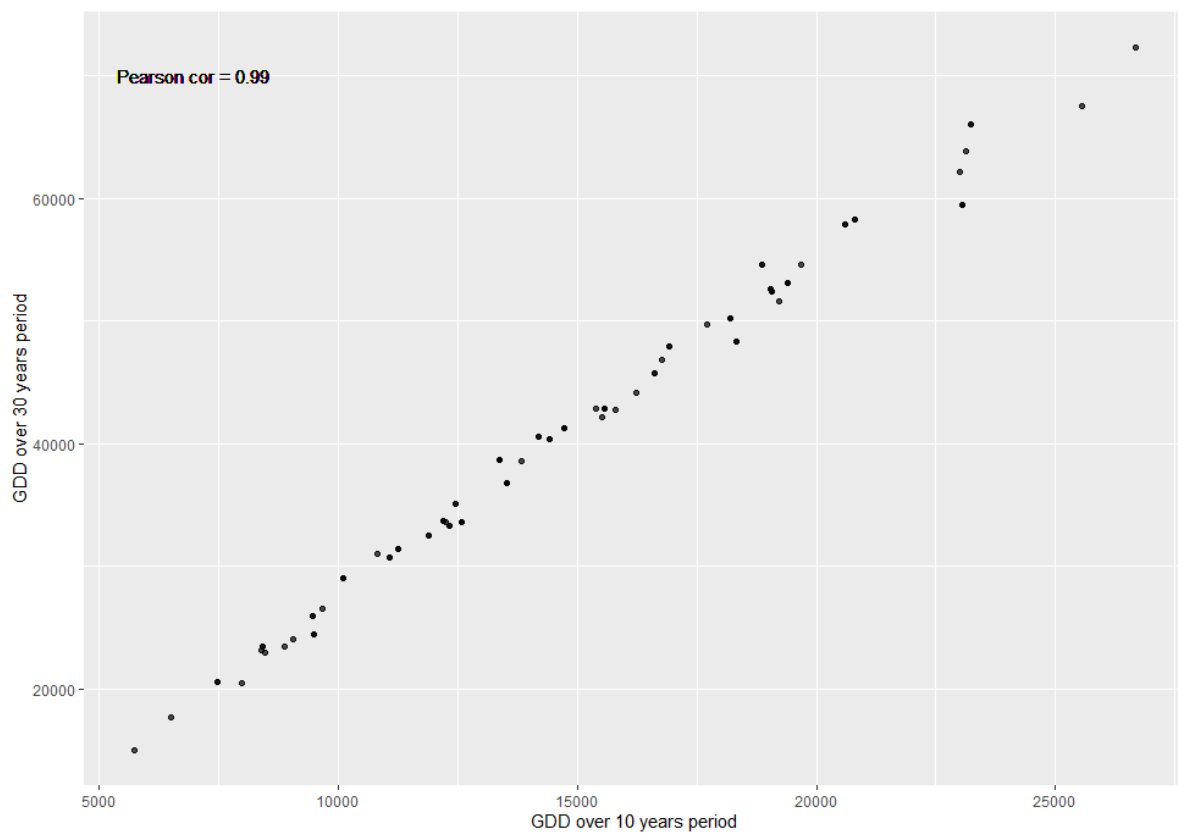


Figure S7: Comparison of growing degree days (GDD) calculated over 30 years and GDD calculated over 10 years.

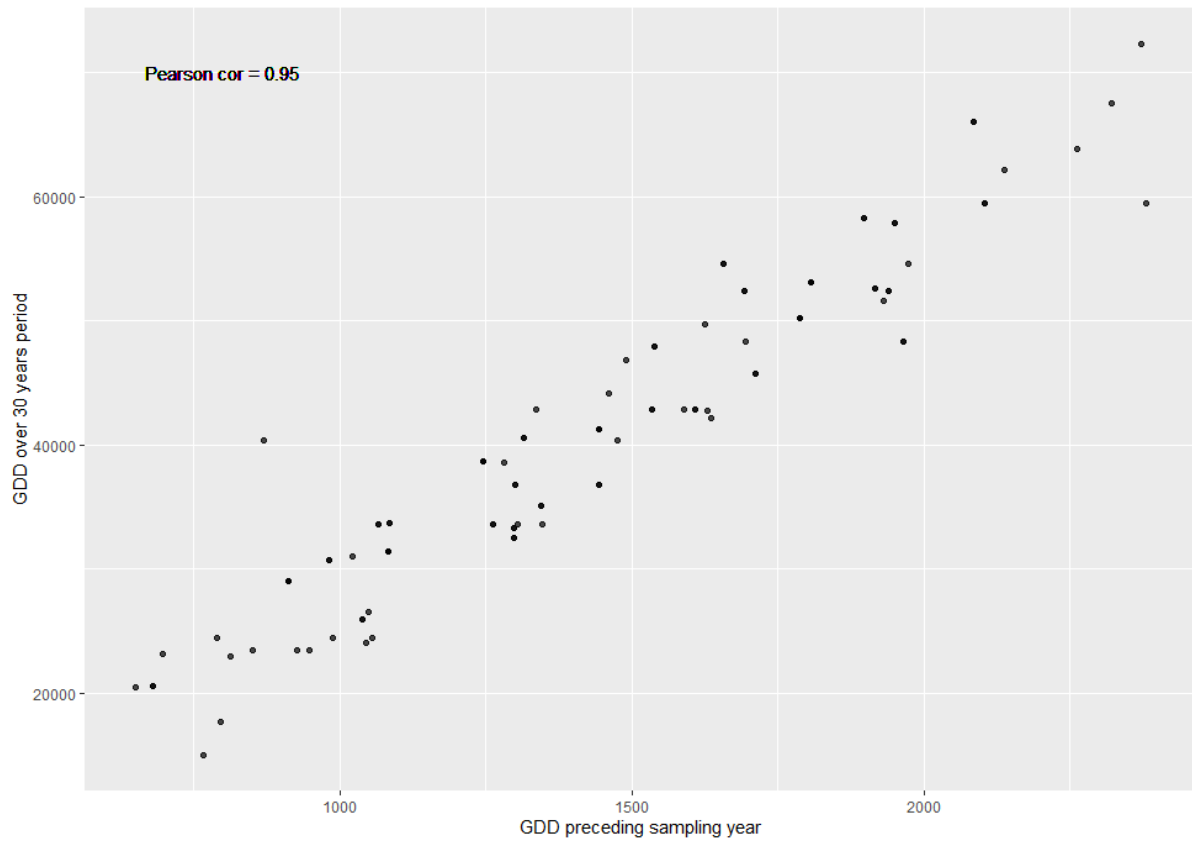


Figure S8: Comparison of growing degree days (GDD) calculated over 30 years and GDD calculated over the year preceding sampling on Orchamp plots.

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Résumé

Mes travaux de thèse visent à mieux comprendre les liens entre l'environnement, la diversité des communautés de plantes et du sol, et le fonctionnement des écosystèmes de montagne.

Dans un premier chapitre, nous quantifions l'importance relative des changements environnementaux et de composition de la communauté de plantes et du sol sur des fonctions écosystémiques. Nous montrons l'influence de certains groupes clés (ex. les champignons saprophytes) sur la productivité et la multifonctionnalité de l'écosystème, et le rôle indirect joué par d'autres groupes trophiques qui interagissent avec les champignons saprophytes. Ce chapitre suggère toutefois l'existence d'une régulation de la diversité et de l'activité des groupes de décomposeurs (bactéries et champignons), via leur interaction avec les groupes trophiques qui les consomment. Dans un second chapitre, nous intégrons donc le réseau trophique du sol dans la modélisation de la décomposition de la matière organique à l'aide d'un modèle d'équations structurelles. La prise en compte hiérarchique de l'effet de l'environnement et du réseau trophique sur une fonction donnée ouvre ainsi la voie à des prédictions spatiales du fonctionnement des écosystèmes. Cependant, cette vision hiérarchique, top-down, est difficile à appliquer quand il existe des rétroactions entre les fonctions écosystémiques et les groupes trophiques. Ainsi, dans un troisième chapitre, nous identifions quels aspects de la communauté microbienne (ses traits ou sa fonction), permettent le mieux de prédire les distributions des plantes. Ce chapitre, qui révèle que l'effet de l'activité de décomposition microbienne est un bon prédicteur des distributions des plantes, ce qui n'est pas le cas des traits microbiens liés à l'acquisition des ressources, nous conduit dans un quatrième et dernier chapitre à explorer les associations biogéographiques entre traits et fonction des organismes décomposeurs, et traits et fonction des plantes sans a priori hiérarchique. Nous confirmons ainsi l'importance de la qualité de la litière pour faire le lien entre les compartiments sous et sur le sol à large échelle.

Cette thèse à l'interface entre la biogéographie fonctionnelle, l'écologie des réseaux et l'écologie des communautés a permis de mieux appréhender les liens étroits et multidirectionnels entre les différents compartiments du système plantes-sol et de son fonctionnement.

Abstract

My PhD thesis aims to better understand the links between the environment, plant and soil community diversity, and the functioning of mountain ecosystems.

In the first chapter, we quantify the relative importance of environmental and compositional changes in plant and soil communities on ecosystem functions. We show the influence of some key groups (e.g. saprophytic fungi) on ecosystem productivity and multifunctionality, and the indirect role played by other trophic groups that interact with saprophytic fungi. However, this chapter also suggests that the diversity and the activity of decomposer groups (bacteria and fungi) could be regulated via their interaction with the microbe-feeding trophic groups. In a second chapter, we thus integrate the soil food web into the modelling of organic matter decomposition using a structural equation model. The explicit consideration of a hierarchical structure between the environment and the soil food web on the targeted function should now pave the way for better and more robust spatial predictions of ecosystem functions. However, this hierarchical, top-down view is difficult to apply when there are feedbacks between ecosystem functions and trophic groups. Thus, in a third chapter, we identify which aspects of the microbial community (its traits or its function) best predict plant distributions. This chapter reveals that the effect of microbial decomposition activity is a good predictor of plant distributions, which is not the case for microbial traits related to resource acquisition. In a final chapter, we therefore explore the biogeographical associations between traits and functions of decomposer organisms and traits and functions of plants without any prior hierarchical structure. We thus confirm the importance of litter quality in linking the below- and aboveground compartments on a large scale.

This thesis at the interface between functional biogeography, network ecology and community ecology has allowed us to better understand the close and multi-directional links between the different compartments of the plant-soil system and its functioning.

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Aux esprits aiguisés qui, en s’amusant constamment à secouer mes certitudes sur la vie - je parle à la fois de ma vie et de celle que tout biologiste cherche à comprendre - m’ont amenée à la science, à la recherche, à tant aimer comprendre, questionner, démonter, observer, calculer, conceptualiser, lier, rassembler et tout recommencer. Il y a bien sûr mes parents, enfin là surtout mon père, pour qui toute idée doit s’accompagner d’un plan, et tout futur plan d’un grand questionnement sur les fondements. Mais quelque part, dans les nuances de ma thèse, il y a certainement aussi un peu l’empreinte de mon Oncle Steve et sa femme Chantal, mes grands modèles d’amour de la science, d’amour de la vie, et d’amour tout court.

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... et puis à ceux qui m’ont sauvée des insomnies pleines de code, épuisée que j’étais du vélo, de l’escalade, de la marche, de la course ou de ne pas avoir réussi à bouger de la journée tant on discutait. Cela comprend mes petites sœurs depuis toujours, et puis Lucile, Gomar, Aurore, Seb, Jil, Charlotte, Léonore. Mais depuis que je suis à Grenoble, il y a aussi Jacques, Nate, Amber, Jonathan, Félix, Eirik, Natasa, Isabelle ; et Micha, pour m’emmener en rappel jusqu’à la mer, et remonter sans sentier.

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