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Rhizodeposition and litter across the Plant Economic Space:implications for soil food web energetics and organic matter cycling

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« Le doute est une force. Une vraie et belle force. Veille simplement qu'elle te pousse toujours en avant. »
- Pierre Bottero, *Ellana*

Rhizodeposition and Litter across the Plant Economic Space: Implications for Soil Food Web Energetics and Organic Matter Cycling

Chloé Folacher

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General introduction

1. Living soil

1.1. Soil and ecosystem services

Human societies are currently facing two major threats: unprecedented rates of climate change and biodiversity loss, under anthropic influence. Soils are pivotal to ecosystems: they are both the largest soil repository of organic matter on land (4150 GtC ± 650, namely, more than the carbon stored in the atmosphere and vegetation biomass together; Lehmann & Kleber, 2015), and the most diverse habitat with 59 ± 15% of all living species *"rely[ing] on soil to grow, compete and complete their life cycle"* (Anthony et al., 2023). Because soils, when considering only the belowground plant parts, cannot assure the primary productivity functions, some have argued that it should be considered as an ecological system, but not an ecosystem (Gobat et al., 2010). In the rest of this manuscript, in order to avoid this discussion, the term "soil ecosystem" will refer to the plant/other biota/soil system, coherent with the Millennium Ecosystem Assessment (2005)'s definition of an ecosystem as "*a dynamic complex of plant, animal, and microorganism communities and the non-living environment interacting as a functional unit*".

Soils are defined by Soil Science Society of America as *"layer(s) of generally loose mineral and/or organic material that are affected by physical, chemical and/or biological processes at or near the planetary surface and usually hold liquids, gases and biota and support plants*" (van Es, 2017). They are characterised by their situation at the interface between mineral and organic compartments, and a complex organisation across spatial (from microaggregates to drainage basin) and temporal (from immediate chemical reactions to geological bedrock alteration) scales (Gobat et al., 2010).

Major soil functions through which soil contributes to ecosystem services include primary productivity, water quality regulation, climate regulation, biodiversity reservoir and nutrient cycling (Lehmann & Kleber, 2015). Other soil processes beyond the scope of this manuscript also provide supporting services such as provision of habitat, as well as a wide range of cultural services, including the preservation of cultural heritage. Multifunctionality is the ability of a soil to sustain different functions at a relatively high level (Zwetsloot et al., 2021). However, because of trade-offs between these functions, only few ecosystems can provide each function at a high level. Zwetsloot et al. (2021) have shown that climate regulation, biodiversity and nutrient cycling were less frequently delivered at high capacity in European grasslands and croplands than other functions. This highlights the room for improvement of ecosystem management, considering the climate and biodiversity crises.

Biodiversity includes, in its broader definition, the variability of living organisms across different scales (from genes to ecosystems), including biotic interactions and interactions of organisms with their environment, as well as ecological and evolutionary processes. The insurance hypothesis (Yachi & Loreau, 1999) states that higher biodiversity is a protection against decline in ecosystem functioning, thanks to higher possible compensation for a diminution in a species' relative contribution to an ecosystem process.

The Jenga™ analogy for functional diversity (Figure 1) illustrates how the realisation of a function can be impervious to moderate loss of taxonomic diversity (b), rely disproportionately on some species (c) or depend on a critical number of species performing the processes, which leads to system collapse (d) if they are removed. As such, threats to soil biota are direct risks for soil functions, and Orgiazzi et al. (2016) evaluated that fourteen countries in the European Union have more than 40% of their soils with moderate-high to high potential risk for soil functions (Figure 2).

Soils have also been described as *"the most difficult"* ecosystem to study by De Ruiter et al. (2005). Hurdles to overcome include high spatial variability at different scales, complexity of continuous monitoring of soil parameters, and limited knowledge on soil biodiversity (Scheffers et al., 2012), with for example only 1% of species of Nematoda, Bacteria and Fungi described (up to 17% for Collembola, and 55% for Acarii, but only 23% for earthworms).

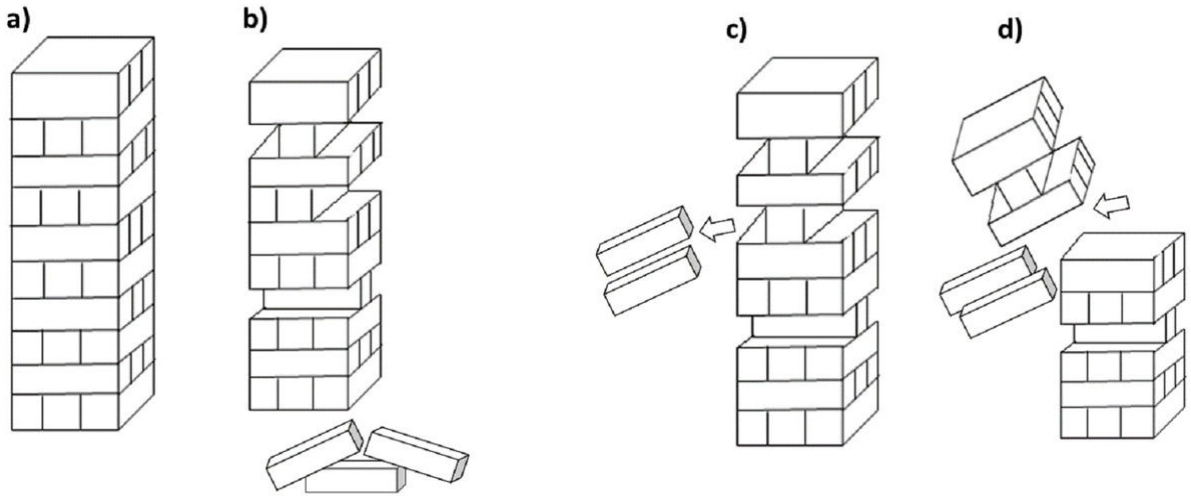


FIGURE 1 Jenga™ analogy for functional diversity (Tibbett et al., 2020)

(a) A stable tower represents the function of the system and each of the blocks represent a species, a number of species in the system contribute to the function; (b) some species can be removed during a disturbance but the overall function of the system can still be maintained (i.e. some bricks can be removed without the tower falling) however (c) some species may have more importance in maintaining the function compared to others, or there may be a critical limit where too many species are removed which will lead to (d) collapse of the systems function.

This leads to real difficulties in the estimation of soil biota sensitivity to anthropogenic pressures. Recent assessments of risks to soil biodiversity found that soil biodiversity is predominantly threatened by intensive land exploitation, including both organic matter stock decline in relation to agricultural practices and land use change (Gardi et al., 2013; Orgiazzi et al., 2016). As soil organisms are key players in soil functioning, soil biodiversity is increasingly recognised as a capital resource for soil security (McBratney et al., 2014), a cornerstone of various societal challenges including water, food and energy security.

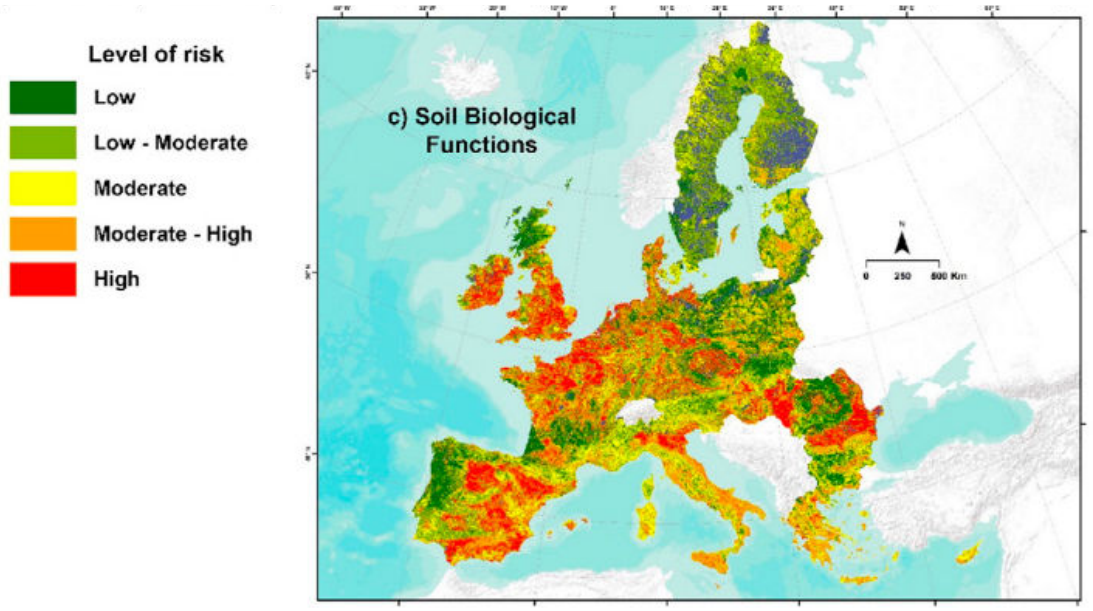


FIGURE 2 Map of potential risk to soil biological functions in Europe (Orgiazzi et al., 2016)

1.2. Soil Food Webs and ecosystem processes

From microbes that have been formally included in carbon cycle models (e.g. in the millennial model or in MIMICS, Abramoff et al., 2018; Wieder et al., 2014, 2024) to the development of countless biological indexes to assess "soil health" or "soil quality" including multiple faunal groups (Creamer et al., 2022), soil biological components have been gaining renewed attention in the past years, in relationship to multifunctionality assessment (Figure 3).

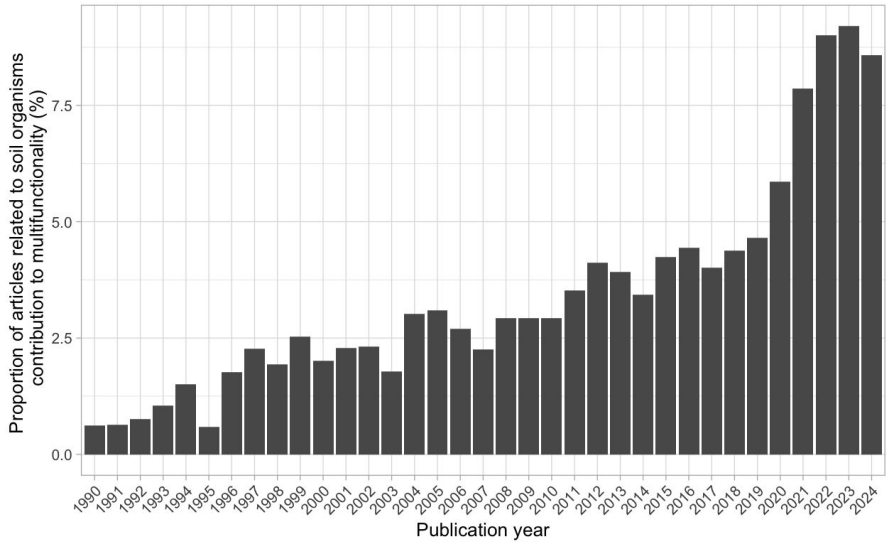


FIGURE 3 Evolution of the attention to soil organisms in relation to multifunctionality in soil ecology

The proportion is calculated as the number of articles returned by the query TOPIC:(soil organism OR soil biota OR soil fauna) AND (multifunctionality OR soil functioning) normalised by the number of articles returned by the query: WEB OF SCIENCE CATEGORIES: (Environmental Sciences OR Soil Sciences) AND Ecology. Selected WOS categories are the top 3 categories from the first query.

1.2.1 Soil organisms and ecosystem functions

Creamer et al. (2022) identified four ecosystem functions that can be influenced by soil organisms (see Table 1): water regulation, carbon and nutrient cycling, climate regulation and disease and pest regulation. Each function is characterised by subfunctions – for example nutrient transformation, reallocation or assimilation are subfunctions of nutrient cycling –, which are influenced by soil processes. Focussing on plants, microbes, nematodes, springtails and mites, we will browse their participations to soil processes, particularly through their trophic interactions.

Plants

Plants are autotrophic multicellular eukaryotes with specialised tissues and organs, capable of photosynthetic nutrition. We will focus on vascular plants, though mosses can also have a tremendous influence in some ecosystems (Nilsson & Wardle, 2005).

Plants are essential to soil ecosystems, both as primary producers (for their above-ground parts) and as ecosystem engineers. They provide soil food webs with several plant-derived resources (Cebrian & Lartigue, 2004):

- roots, eaten by herbivores and plant-parasites;
- litter, the senesced plant tissues (either from above or belowground organs), that sustain the detritivores and decomposers;
- rhizodeposits, the mix of exudates and leachates from roots, that provide easily available carbon and energy to microorganisms of the rhizosphere.

Root systems affect substantially all four aspects of ecosystem functioning (Table 1). Their influence even goes beyond the processes presented in Table 1 (aggregation, exudation, macropore formation, nitrogen transformation, plant metabolic enhancement and root foraging): indeed, roots also contribute to nutrient cycling through bedrock weathering and to water regulation through hydraulic redistribution and evapotranspiration, but also to the regulation of soil erosion (Freschet, Roumet, et al., 2021).

Roots themselves contribute to water circulation through the formation of macropores and to nutrient cycling by nitrogen absorption. Rhizodeposits not only contribute to carbon and nutrient cycling (more on that point in §3.2) but also favour soil aggregation, and have a selecting effect on rhizosphere's microorganisms (Yan et al., 2017).

The quality and quantity of root tissue, litter and rhizodeposits, as well as the timing of their delivery depends on plant species identity. Leaves, stem and roots properties (morphological, physico-chemical) variation across plant species are not random but coordinated, and reflect plant strategies for resource acquisition (§3.1). Plant properties can have strong impacts on higher trophic levels.

TABLE 1 Overview of the links between soil living organisms and soil processes in relation to four soil functions: water regulation (blue), nutrient cycling (purple), carbon and climate regulation (grey) and disease and pest regulation (green), extract from Supp. Info. in Creamer et al. (2022).

When applicable specific actor groups are given between brackets, in which feeding groups are abbreviated as (bactivorous (B), fungivorous (F), mycorrhizal (M), omnivorous (O), predatory (Pr), parasitic (Pa), saprotrophic (S)). Enz. refers to specific enzymatic machinery. Processes directly related to trophic interactions are shown in bold. Colour intensity indicates the strength of available evidence to support a link.

Group	Specific entity in the group	*Process*	Infiltr. & percolation	Water storage	Biological retention	Nutrient transf.	Nutrient realloc.	Nutrient assim.	Decomposition	Ressource realloc.	Biochemical transf.	Disease/pest control	Plant health prom.
Plant roots		*Aggregation*											
		Exudation											
		Macropore formation											
		Nitrogen transformations											
		Plant metabolic enhancement											
		Root foraging											
Bacteria	Bacteria	*Aggregation*											
		Bioaccumulation											
		Exudation											
		Food web assimilation											
		Microbial respiration											
		Mineralisation											
		Competition											
		Antibiosis											
	Growth Promoting Bacteria	*Resistance & defence*											
		Plant metabolic enhancement											
	Bacteria with S-reducing/S-oxidising enzymes	*Sulphur transformations*											
	Bacteria with nitrifying, denitrrifying enzymes	*Nitrogen transformations*											
	Bacteria (Pa)	***Parasitism***											
	Bacteria (N-fixing) mutualistic & free-living	***Nitrogen fixation***											
Fungi	Fungi	*Aggregation*											
		Exudation											
		Mineralisation											
		Microbial respiration											
		Food web assimilation											
		Antibiosis											
		Competition											
		Nitrogen transformations											
	Growth Promoting Fungi	*Resistance & defence*											
		Plant metabolic enhancement											
	Fungi (Pa)	***Parasitism***											
Nematodes	Nematodes (B, F, O, Pr)	***Food web assimilation***											
	Nematodes (B, F, O)	***Microbial grazing***											
	Nematodes (O, Pr)	***Predation***											
	Nematodes (Pest Pa.)	***Parasitism***											
	Nematodes (Plant Pa.)	*Resistance & defence*											
Collembola	Collembola	***Bioaccumulation***											
	Collembola (B, F, O Pr)	***Food web assimilation***											
	Collembola (B, F, O)	***Microbial grazing***											
	Collembola (O, Pr)	***Predation***											
Acari	Acari (B, F, O)	***Microbial grazing***											
	Acari (F, O, Pr)	***Food web assimilation***											
	Acari (O, Pr)	***Predation***											

Microorganisms

Soil microorganisms include bacteria, archea, fungi and protists. We will focus on bacteria and fungi, though protists also participate to the processes we are interested in, such as nutrient mineralisation (Geisen, 2016).

Both fungi and bacteria also impact all four aspects of ecosystem functioning (Table 1). The influence of microorganisms on ecosystem functioning depends on their characteristics such as their carbon use efficiency, their life-form (free-living, symbionts, parasites, whether they form hyphae, …) and their enzymatic arsenal. Their wide enzymatic capacities are essential for carbon and nutrient cycling processes (more details in §2.1.2): they are the main decomposers. Because they function with external digestion[1], their resources are public goods, and biotic interactions are essential regulators of the microbial population (Richards et al., 2018). Their mucilage and/or hyphae contributes to soil aggregation, thus participating to water circulation, while the microbial community is essential for plant health, as there are both symbionts/plant-growth promoting microorganisms, but also parasites.

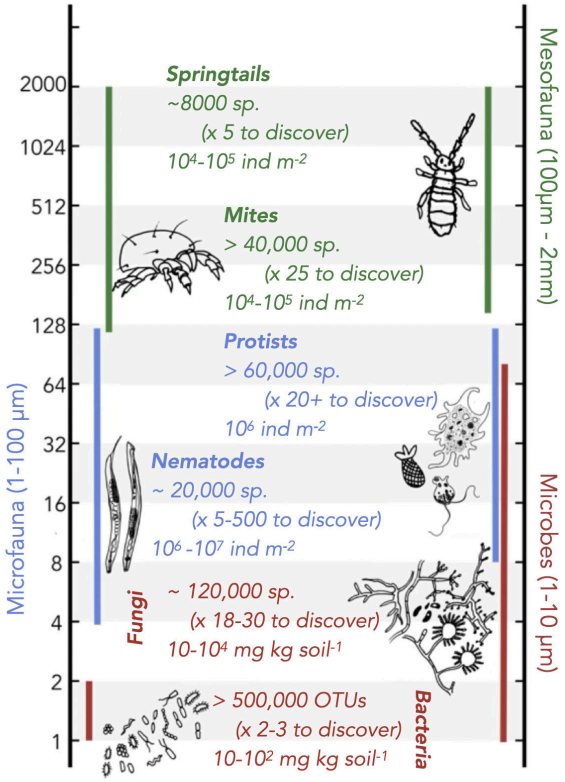


FIGURE 4 Overview of soil organisms' size, richness and abundance

Modified from Martinez Almoyna (2021). Known specific richness and estimation from Thibaud & D'Haese (2010); Walter & Proctor (2013); Adl et al. (2007); Poinar (2012); Hawksworth & Lücking (2017); Louca (2019), for springtails, mites, protists, nematods, fungi and bacteria, respectively. Animal and microbial groups density from Petersen & Luxton (1982) and He et al. (2020).

Bacteria are microscopic unicellular prokaryotes lacking membrane-bound organelles in their cell organisations. Their cells are generally considerably smaller than eukaryotic cells. They have a variety of shapes (mostly spherical, rodlike, or curved but also various other including corkscrew-like morphology or helical forms) and multi-organism structures (pairs, random clumps, chains or even hyphae-like structures).

2% of bacterial phylotypes accounts for half the soil bacterial communities worldwide (Delgado-Baquerizo et al., 2018). The common phylotypes are often the dominant ones, and they belong to the phyla Proteobacteriota (***α*** et ***β***), Actinomycota, Acidobacteriota and Planctomycota. Delgado-Baquerizo et al

[1] Most decomposition processes are mediated by exoenzymes, catalysing the extra-cellular depolymerisation of organic matter (§2.1.2).

(2018) highlighted the importance of plant productivity, alongside climatic factors and soil pH, to predict the ecological preferences of these dominant phylotypes.

The copiotroph-oligotroph continuum describes bacterial traits relative to growth (Fierer et al., 2007). Copiotrophic bacteria thrive in the rhizosphere and surface soils, where they are competitive for acquiring readily available carbon from rhizodeposition and using this carbon source to fuel a high growth rate despite low carbon use efficiency. On the other hand, oligotrophic bacteria are found in the bulk soil and sub-soil, where they grow slowly, but with a higher carbon use efficiency. Since the development of metagenomics 16S analysis, there have been various attempts to classify bacterial phyla in one category or the other (Fierer et al., 2007; Ho et al., 2017, see Figure 5), as there is a phylogenetic signal of growth rate (Walkup et al., 2023). However, to accurately predict life history strategies, phyla appear less accurate than lower levels of classification such as families or genera (Dragone et al., 2024; Stone et al., 2023).

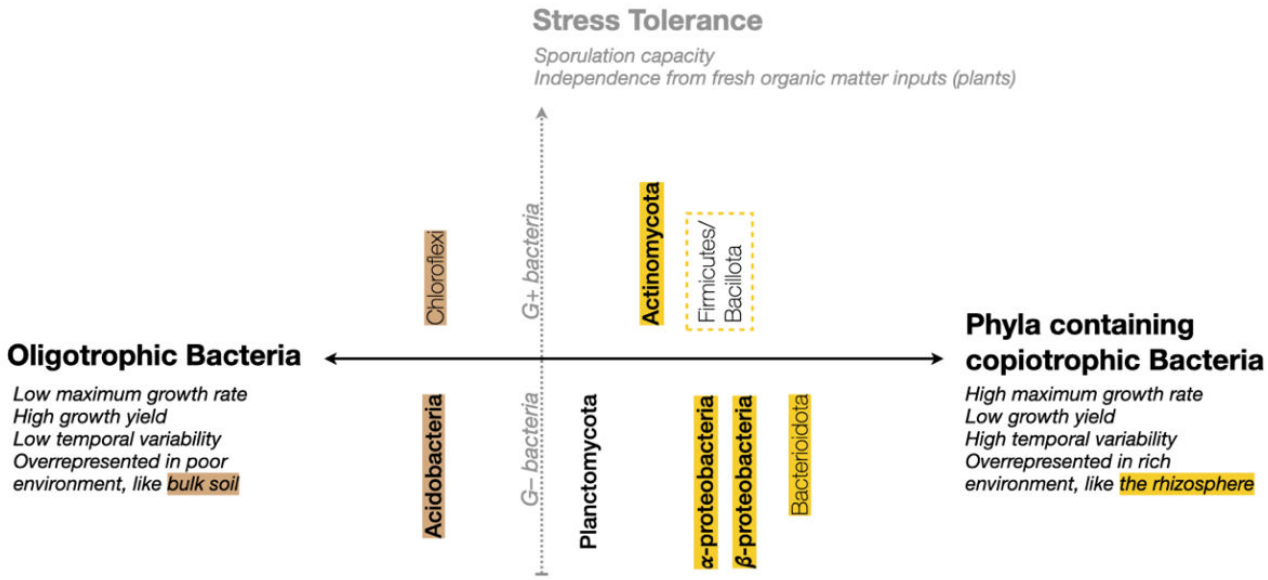


FIGURE 5 Simplified overview of bacterial phyla (or classes) life history strategies

Overall, most soil bacterial strains seem to be oligotroph. Interestingly, copiotrophs seem to be found only in some phyla, including Actinomycota, Bacterioidota and Proteobacteriota (Stone et al., 2023), which are often over-abundant in the rhizosphere compared to bulk soil. However, even if broad categories lack precision, they can still be useful to assess ecological functioning, even without metabarcoding, as the Gram-positive (G+) to Gram-negative (G–) bacteria ratio (see Box 1) is well correlated to the oligotrophic:copiotrophic bacteria ratio (Orwin et al., 2018). The distinction between G+ and G– bacteria is based on the structure of their cell wall. These structural disparities are associated with functional differences: the G+:G– ratio has also been successfully linked with carbon use and ecosystem functioning, such as productivity (Fanin et al., 2019). G+ bacteria (Actinomycota, Bacillota) tend to be more dependent on complex molecules, while G– bacteria have been shown to be more associated with rhizospheric carbon

(ibid). The G+:G– ratio is also an indicator of stress resistance; because of their sporulation capacity, G+ bacteria tend to be more tolerant to droughts or flooding (De Vries & Shade, 2013).

Box 1: Phospholipid fatty acids (PLFA) analysis

Phospholipid fatty acids are cell membrane components of bacteria and eukaryotes. As they do not accumulate in SOM, they are interesting biomarkers for soil microbial biomass (Frostegård et al., 2011). Interestingly, the composition of phospholipids in the membrane varies across microbial groups, and despite very few phospholipids being exclusively specific of one group, it is possible to use some as coarse indicators for the relative abundance in G– bacteria, Firmicutes (G+), Actinomycetes (G+), AMF, Ascomycota and Basidiomycota and Zygomycota (Joergensen, 2022). Specific group biomarkers are listed below:

AMF	16:1ω5*
ASCOMYCOTA AND BASIDIOMYCOTA	18:2ω6,9
ZYGOMYCOTA	18:1ω9
G– BACTERIA	cy17:0; cy19:0; 16:1ω7; 16:1ω9; 17:1ω8; 18:1ω7
FIRMICUTES (G+ BACTERIA)	i14:0; i15:0; i16:0; i17:0, i18; a15:0, a16:0; a17:0; a18:0; a19:0
ACTINOMYCETES (G+ BACTERIA)	10Me16:0, 10Me17:0; 10Me18:0

**In the X:YωZ nomenclature (Norris et al., 2023), X refers to the length of the carbon chain, Y to the number of double bonds, and Z indicates the position of the double bond, counting from the end of the carbon chain (not from the carboxyl group). Prefix i and a refer to a methyl group branching off the second (iso) and third (anteiso) carbon from the end of the carbon chain, respectively. Prefix 10Me refers to a methyl group branching off the tenth carbon from the carboxyl group. Prefix cy describes an unsaturation by a chain instead of a double bond.*

Because they do only reflect relative abundances (the concentration in PLFA varies greatly between groups), they are often used by calculating ratios, for example fungal:bacterial PLFAs ratio or G+:G– PLFAs ratio. Other phenotypic ratios include the **adaptation response ratio** based on anteiso:iso PLFA, the **branch response ratio**, based on the relative abundance of 10Me16:0 and 16:0 (generic bacterial PLFA), both reflecting variation in membrane fluidity, the **metabolic response ratio**, based on the relative abundance of cy:17 and 16:0, reflecting carbon availability, and the **stress response ratio**, based on the relative abundance of cy19:0 and cy19:0 (Norris et al., 2023).

Fungi are uni- or multicellular eukaryotes, with an eluding definition as their differentiation with protist is blurred (Richards et al., 2018). They tend to have a rigid cell wall containing chitin and ß-glucan. Ascomycota is both the most diverse phylum[2] of fungi and the dominant phylum at the global scale (Egidi et al., 2019), including generalist saprotrophs but also parasitic fungi. Along with Basidiomycota (a phylum that tends to be dominant at the local scale (ibid) and includes major ectomycorrhizal and pathogenic groups, and most carpophore-forming species), and Entorrhizomycotina (a small plant endophyte phylum), they form the Dikarya sub-kingdom (Naranjo-Ortiz & Gabaldón, 2019). They represent the most recent branch of the fungi kingdom, and are sometimes referred to as «higher fungi» because of their well-developed septate hypha. Other fungal taxa were historically classified in the Zygomycota polyphyletic group (in grey in Figure 6), with the exception of Chytridiomycota. The Glomeromycota class

[2] Reminder of basic classification levels: Kingdom > Phylum/Division > Class > Order > Family > Genus > Species.

is of particular interest to this work, as most of its species are involved in arbuscular mycorrhizal associations.

Mycorrhization is the symbiotic association – *sensu* the "long-term, intimate relationship" (van der Heijden et al., 2015) – between a fungus and a plant. Arbuscular Mycorrhizae (AM), characterised by intra-root cortex arbuscules or coils, involve fungi from the Glomeromycota phyla. They are the most ancient and common mycorrhization association (Brundrett & Tedersoo, 2018), present in more than 70% of plant species, both woody and not woody (van der Heijden et al., 2015). Some Basiodiomycota and Ascomycota species can also be involved in other types of mycorrhizae, like Ectomycorrhizae (EcM) that mainly occur in temperate-living shrubs and trees or in symbiosis specific to plant family like Orchidacae and Ericaceae (van der Heijden et al., 2015).

Broad ecological classification of soil fungi usually includes root pathogens, mycorrhizal symbionts and decomposers, but PLFA analysis does not allow for differentiation between pathogens, non-arbuscular mycorrhiza and decomposers (Box 1).

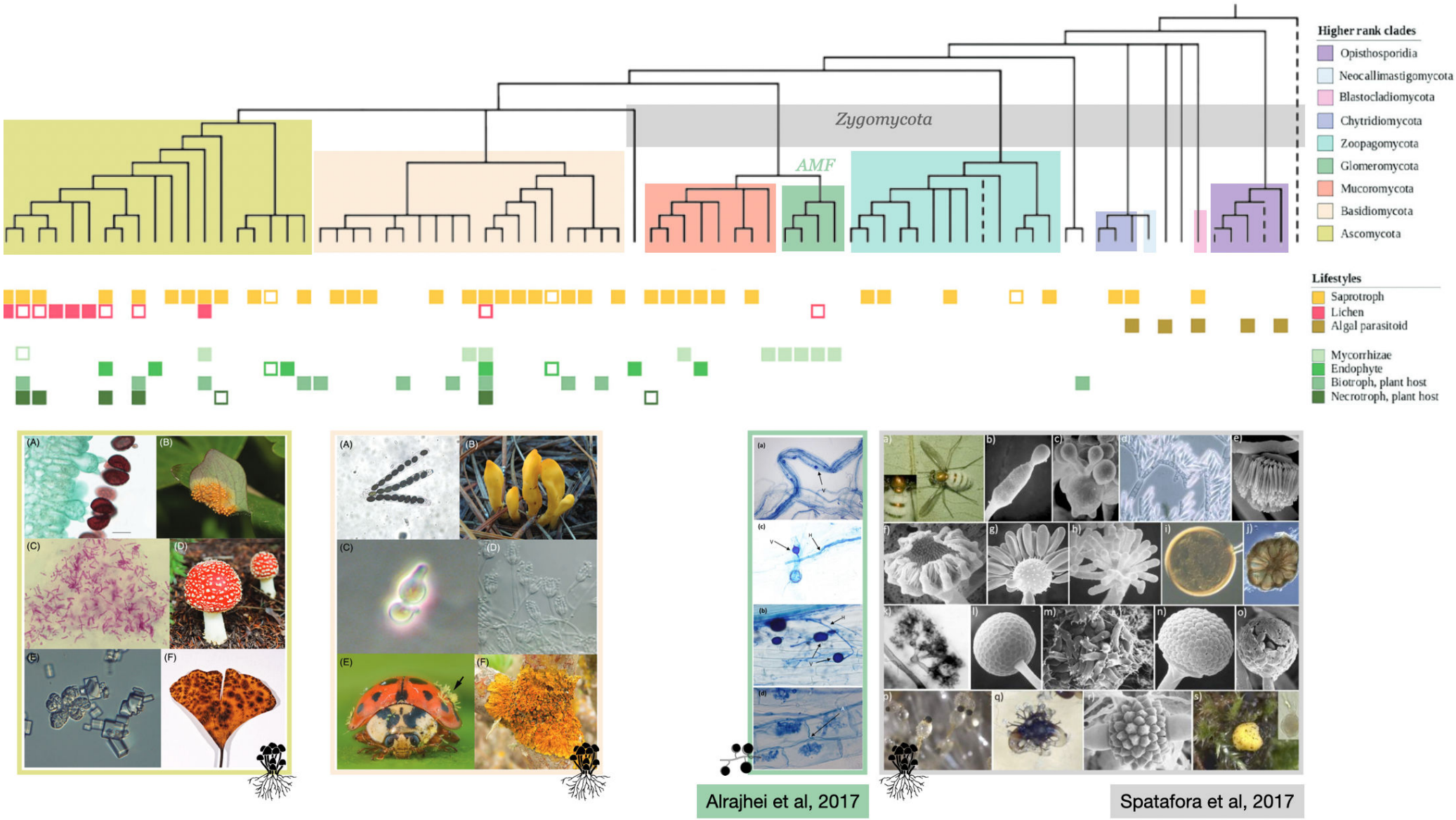


FIGURE 6 Overview of the fungal tree of life (up to class or order level) and broad lifestyle information, modified from Naranjo-Ortiz & Gabaldón (2019)

Lifestyles not shown include animal and fungal parasite as well as commensal fungi. Saprotrophic fungi pictogram by Svenja Meyer, AMF from phylopic (CC BY).

Nematodes and microarthropods

Soil fauna can contribute to all four aspects of ecosystem functioning, but the groups we study here mainly impact soil and nutrient cycles, as well as biotic regulations. The processes these animals participate in are a direct consequence of their trophic interactions (in bold in Table 1). Angst et al. (2024) classified soil fauna influence on the formation and decomposition of soil organic matter (SOM) into three mechanisms: transformation, translocation and grazing (Box 2). While only grazing appear in Creamer et al. (2022)'s synthesis (Table 1), nematodes and microarthropods are actually also involved in transformation and translocation as well, though less so than other faunal groups.

Box 2: Mechanisms through which soil fauna impacts formation and decomposition of SOM (Angst et al., 2024)

TRANSFORMATION is mainly carried out by litter ingestion, digestion and faeces production, processes altering litter physico-chemical properties (mostly undertaken by macro-detritivores, who are beyond the scope of this manuscript).

TRANSLOCATION occurs in different forms. If the role of earthworms (and ants and termites) in bioturbation is well described, nematodes and microarthropods also participate in the translocation of SOM, by affecting the fluxes of dissolved organic matter. Those nutrient-rich leaches can affect the organic matter cycling both directly by sorption/desorption on reactive mineral surfaces and indirectly by alleviating microbial nutrient limitation. The authors also classified the vertical and horizontal transport/dispersion of microorganisms in translocation.

GRAZING on microorganisms by fungivores and bacterivores affect the equilibrium between microbial groups, for example by favouring bacteria over fungi (see §1.2.2 for subsequent consequences on SOM cycling).

Soil nematodes, microscopic worm-shape invertebrates living in soil water films and water-filled pores, are a very diverse phylum encompassing various trophic levels. They can be classified into trophic guilds, based on their mouth parts' anatomy (Figure 7), which is very useful because their influence on ecosystem processes mainly depends on their trophic position. Microbivores play an essential role in releasing the nutrients immobilised in the microbial biomass (see Box 3, Trap et al., 2016) thus indirectly promoting plant growth, while herbivores and phytoparasites directly affect plant growth negatively. By increasing rhizodeposition and carbon allocation to roots, herbivorous nematodes have also been reported to indirectly promote plant growth too (Bardgett et al., 1999).

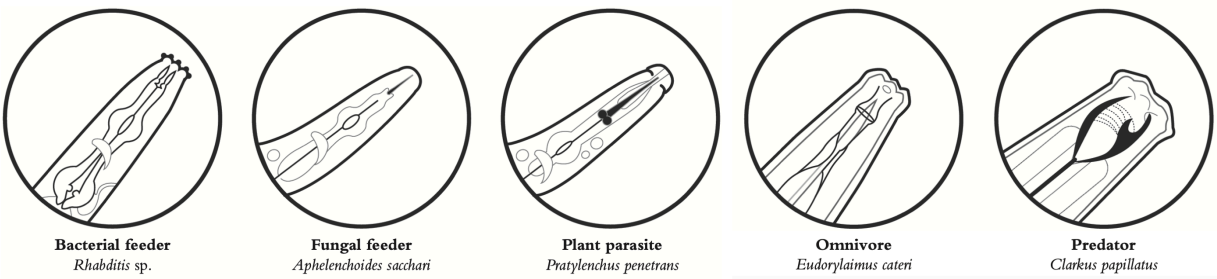


FIGURE 7 Schematic diagram of the main nematode-feeding types based on common nematode species (Nielsen, 2019)

Springtails (class: Collembola) and mites (class: Arachnida) are ubiquitous soil dwelling microarthropods (phylum: Arthropoda). With a size up to 5 mm, and 10^4-10^6 individuals per m^2 (Petersen & Luxton, 1982, Figure 4), they are the most abundant and diverse organisms of soil mesofauna (Nielsen, 2019).

Springtails are hexapods, predominantly fungivorous. As unsclerotised microarthropods, they are an excellent prey, supporting not only predatory mites (Figure 9) but also a wide range of other predators such as spiders or pseudo-scorpions (A. M. Potapov et al., 2021, 2022). Thus, they occupy a key position in the trophic network, between microorganisms and higher trophic levels (meso- and macrofauna predators). Like microfauna (e.g. nematodes, protists), they are efficient regulators of microbial populations, and as such, they participate in nutrients and carbon cycling in the rhizosphere, as well as disease and pest regulation through their trophic interactions (Table 1). Their contribution to the latter service also includes the dispersion of microbes and non-vascular plants (such as algae and mosses). Though it is not included in Creamer et al. (2022)'s synthesis, there are also evidence of their engineering potential with reported (direct and indirect) effects on soil aggregation (Maaß et al., 2015; A. M. Potapov et al., 2020), but the extent of their impact has yet to be quantified. They are usually classified into three life-forms (Figure 8, A. A. Potapov et al., 2016), based on morphological traits and colour. Surface dwelling epedaphic springtails have longer legs and antenna, developed ocelli and tend to be colourful. Soil dwelling euedaphic springtails have short legs, almost no antenna and ocelli and tend to be transparent. Hemiedaphic springtails have intermediate characteristics. Life form likely influences their contributions to ecosystem functioning, with opportunities for transformation, translocation and grazing depending on their habitat and their mobility.

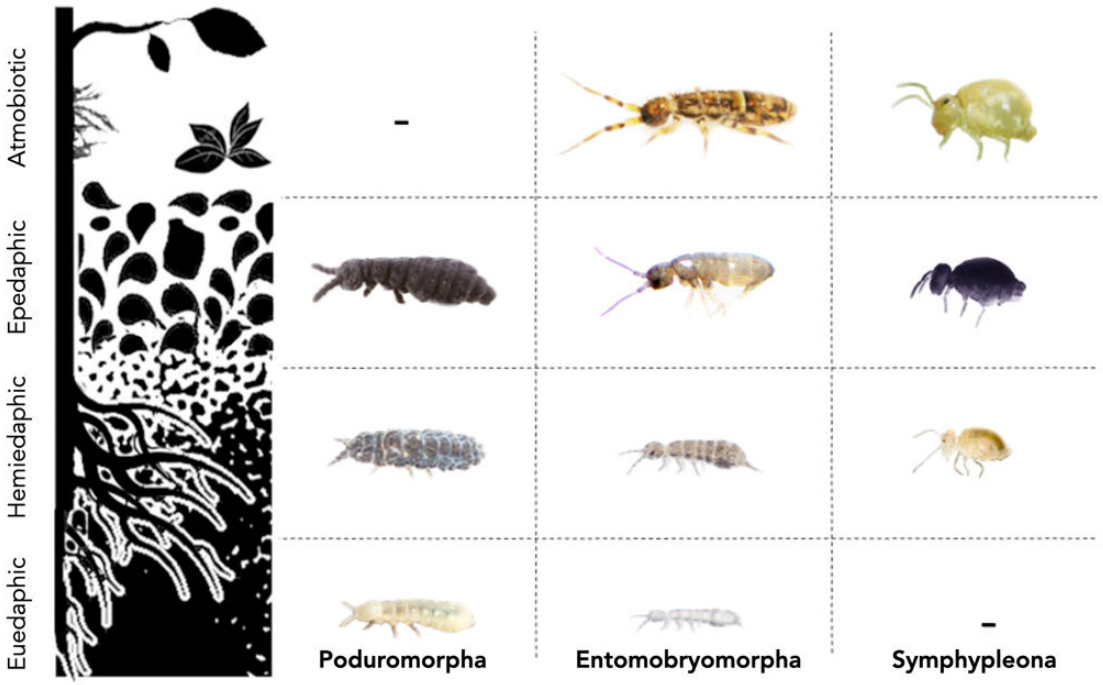


FIGURE 8 General adaptive morphologies in Collembola (A.A. Potapov et al., 2016)

Taxonomic orders in columns and life forms in line.



FIGURE 9 "A Laelapidae, triumphant with its Collembola kill". Tarkine, Tasmania, Oct 2014
© Andy Murray, Chaos of Delight (website)

Mites are arachnids with diverse trophic regimes. Oribatid mites (superorder: Acariformes) are heavily sclerotised saprophages and fungivores. They are usually the most diverse and abundant groups of mites (Nielsen, 2019). As fungivores their contribution to ecosystem functioning is closely related to that of springtails, though they are not such an easy prey. Mesostigmatid mites (superorder: Parasitiformes), on the other hand, are mostly predatory, feeding on springtails and nematodes. They participate in the regulation of microbial grazing by preying on microbivore fauna. Prostigmatid mites (superorder: Acariformes) have diverse feeding type, as this taxon includes herbivores, microbial grazers, decomposers and predators.

1.2.2 Soil Food Webs organisation

As trophic interactions support a large number of processes participating to ecosystem functioning, quantifying energy fluxes into food webs have been highlighted as a strong approach for assessing multifunctionality (Barnes et al., 2018), allowing for the consideration of the ecosystem as a whole rather than studying its components separately. Understanding how the energy and nutrients flow across organisms is a core questioning for ecology as a field (Odum, 1962). However, before the quantification of these interactions, the structure of the trophic network must be resolved. The organisation of food webs components in compartments has occupied modellers for 50 years (May, 1972; Pimm & Lawton, 1980).

In soil food webs in particular, partitioning between fast and slow channels[3] (*sensu* turnover rates or production:biomass ratio, Rooney et al., 2006) has been the subject of much ink. All of the three

[3] In soil food web modelling, a channel refers to the a cluster of trophic links and nodes resulting from web compartmentalisation (A. M. Potapov et al., 2023). More in §1.2.2.

competitive views of soil food web compartmentation identified by Potapov et al. (2023) have their fast and slow channels, though they are not perfectly equivalent.

The distinct plant-derived **resource channels compartmentation (a)** includes a dual detrital network with a (fast) bacterial channel composed of bacteria and bacterivores, dependant on labile substrate, and a (slow) fungal channel (fungi and fongivores), based on recalcitrant substrate and an independent plant based channel (herbivores)[4], all three united together in higher trophic levels (Hunt et al., 1987). The **body size compartments approach (b)** separates a fast channel of small organisms with high turnover, and a slow channel of larger organisms that retain carbon over their longer lifespans (A. M. Potapov et al., 2019, 2020). Finally, the compartments can be also be based on the **spatial separation (c)** of bulk soil (slow), litter (intermediate) and rhizodeposits (fast).

These frameworks can be integrated, the size compartmentalisation may for example be nested within the spatial approach. Compartmentalisation also depends on the explored research issue and on the groups included.

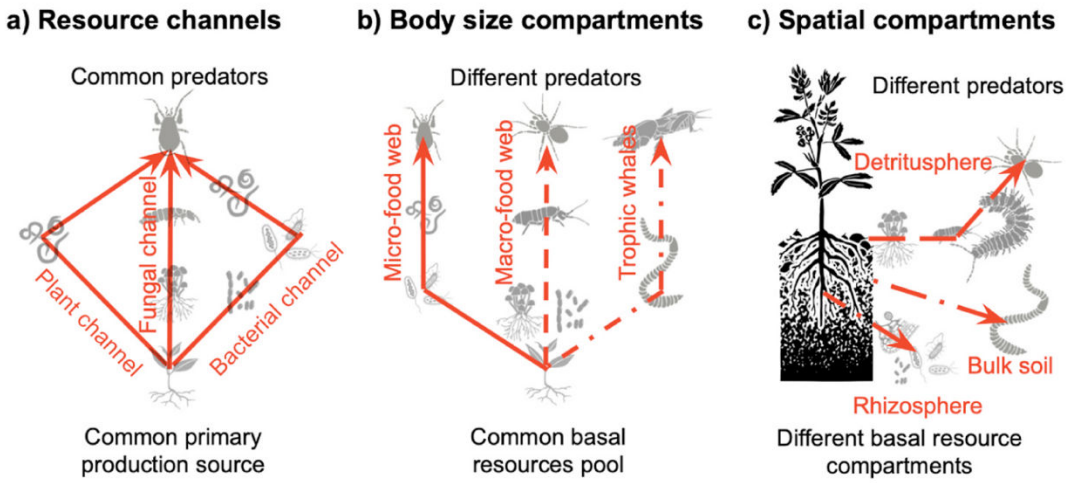


FIGURE 10 Different concepts of soil food web structures (from Potapov et al., 2023)

In our case, integrating basal resources from rhizosphere, detritusphere and bulk soil (c) while considering the separation between fungal and bacterial channels (a), we will cross the "resource channel" and "spatial compartment" approach. The body size compartment approach is irrelevant for this study: as our highest trophic levels are predatory nematodes and mesostigmatid mites, macro-food web and trophic whales are beyond the scope of this study (Figure 11).

[4] In Hunt et al. (1987)'s initial approach, herbivores' « green » channel is separated from detritus-based « brown » channel also because of distinct mechanisms regulating the stability of both networks. Network stability considerations are beyond the scope of this manuscript, but is an active field of research in food web modelling. It is also interesting to note that in their compartmentalisation, labile rhizodeposits are considered part of the detrital basal resources.

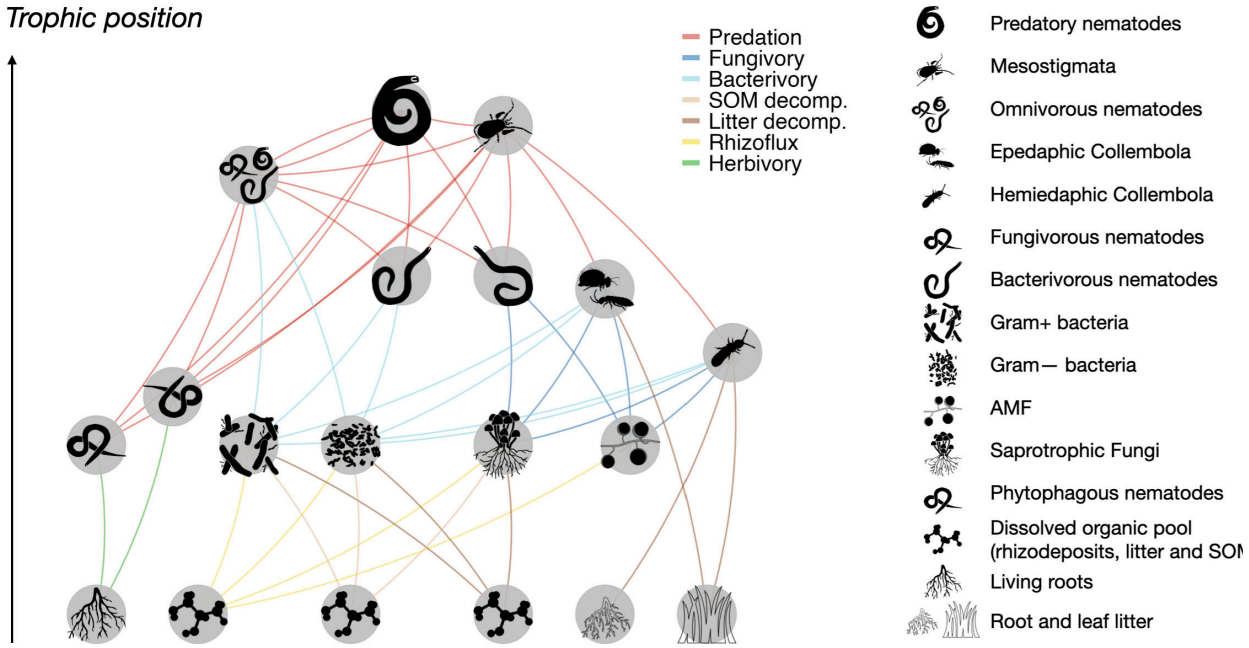


FIGURE 11 Overview of the nature of trophic interactions between the organisms of interest

Pictograms by Svenja Meyer (fungi, nematodes and mesostigmata), Louise Folacher (roots) and phylopic (Creative Commons Attribution License 'CC BY', source: https://www.phylopic.org/).

The dichotomy between fungal and bacterial channels is not only supported by the description of energy fluxes in soil food web estimating the proportion of a species' diet derived from one basal resource or another (Hunt et al., 1987; Moore & Hunt, 1988), but also by different characteristics of the two groups. Indeed:

- bacteria have restricted motility in soil, whereas fungi can explore large soil volumes with their hyphae (though Actinomycota can form filamentous structures, and not all fungal species have hyphae);
- fungi have higher biomass, C:N ratio and carbon use efficiency but lower turnover time and respiration rate (X. Wang et al., 2019);
- the fungal channel is supposed to be more regulated by bottom-up dynamics, while the bacterial channel tends to be more affected by top-down control (Bonkowski et al., 2009), though both fungal and bacterial communities can experience selective grazing by their consumers.

Top Down vs Bottom-up (Dyer & Letourneau, 2003)

BOTTOM-UP DYNAMICS	Resource-based regulation of upper trophic levels
TOP-DOWN CONTROL	Predator-based regulation of lower trophic levels

Their enzymatic capacities also differ (de Boer et al., 2005). For example, while both saprotrophic fungi and some Gram+ bacterial genera (such as *Streptromyces* or *Bacillus*) can degrade cellulose in aerobic conditions, anaerobic and anoxic cellulose degradation is almost exclusively conducted by bacteria. Fungi are nonetheless generally considered to be responsible for the large majority of cellulose degradation, because cellulose is relatively inaccessible to bacteria when crystallised or within a lignocellulose complex. Lignin degradation, on the other hand, is mainly found among certain genera of Basidiomycota, while other fungal groups and Actinomycota species only have the ability to solubilise and modify lignin to gain access to cellulose. Saprotrophic fungi have indeed been associated with higher activity of enzymes involved in lignin and cellulose degradation (Romaní et al., 2006), while bacteria have a range of taxa specialised in nitrogen cycling steps like nitrogen fixation, nitrification (see §2.2), or methanogenesis or methanotrophy (Crowther et al., 2019).

These well-established differences have led to the consideration of bacterial and fungal compartments as basal entities fuelling independent energy channels relying on separate basal resources (Figure 10.a): the bacterial channel being linked to fast cycling of labile rhizosphere carbon while saprotrophic fungi were associated with the decomposition of carbon with a longer residence time.

However, evidence of root-derived carbon's importance for soil food webs (Pausch et al., 2015; Pollierer et al., 2007; Ruf et al., 2006) has led the scientific community to reconsider this consensus. In opposition to Hunt et al. (1987) who classified labile root-derived carbon as detritus, rhizodeposits are increasingly associated with the green channel, because they co-occur with living roots and contrary to most detritus, they are a readily available carbon source.

The rhizosphere community is composed of both fungi and bacteria. While the only fungal group traditionally supposed to rely on root-derived carbon were mycorrhizal fungi (Hunt et al., 1987), findings from the last 20 years show that saprotrophic fungi also incorporate recent photosynthates (Pollierer et al., 2007). On the other hand, G+ bacteria have been found to be specialised in the use of recalcitrant compounds as a carbon source and scarcely absorb recent photosynthates (Kramer & Gleixner, 2008). Without denying the inherent natural differences between fungi and bacteria, nor their interest as rough indicators useful for ecosystem comparison, taking into account rhizodeposits in the context of the very loose feeding preferences of soil animals in the elucidation of the soil food webs compartmentalisation is still an ongoing investigation (Brose & Scheu, 2014; Crotty et al., 2012).

A better understanding of rhizodeposition is not only essential soil food web functioning: rhizodeposits, besides being a key basal resource for both fungal and bacterial channels, also affect soil organic matter cycling, both directly and indirectly.

2. Soil organic matter cycling

Rhizodeposits are increasingly recognised as a key source for soil organic matter (SOM) formation, especially stable, mineral-associated organic matter (MAOM; Sokol, Kuebbing, et al., 2019; Villarino et al., 2021), though their relative importance compared to microbial necromass (Buckeridge et al., 2020) or plant litter (Cotrufo et al., 2015) is yet to resolve (Sokol, Sanderman, et al., 2019; Whalen et al., 2022). In addition, root exudates have been shown to enhance SOM decomposition (positive priming effect), both directly through destabilisation of mineral protection (Keiluweit et al., 2015) and indirectly through higher microbial exoenzyme production fuelled by the easily available carbon from rhizodeposits (Dijkstra, 2007; Mo et al., 2021; Shahzad et al., 2015).

Priming effect describes short term changes in turnover of native SOM in response to the addition of fresh organic materials (Kuzyakov et al., 2000). An example of positive priming effect is the acceleration of native SOM mineralisation under the influence of rhizodeposits. Such acceleration – or *hot moment* –, often triggered by biotic activity (e.g. ingrowth of a root in a given soil volume, litterfall, root death, animal burrow formation), leads to a strong spatial heterogeneity in process rates (up to 100 times higher in the rhizosphere than in the bulk soil, for example). This has been conceptualised as *hot spots* (Kuzyakov & Blagodatskaya, 2015). *Hot spots* include the rhizosphere, the detritusphere, biopores and the aggregates' surface (especially in deeper horizons with less biological activity). Hot spots are where most of the organic matter transformations presented in this section occurs.

2.1. Overview of soil organic matter cycle

2.1.1 Soil organic matter pools

SOM has been classified in different compartments associated with fast or slow turnover time, notably for modelling purposes. Historically, the distinction between fast and slow pools was based on chemical recalcitrance, while turnover time is now believed to depend mostly on protection by adsorption on mineral particles or integration in micro or macroaggregates (Christensen, 2001; Lehmann & Kleber, 2015). This emerging view has led to a new classification of organic matter fractions (Lavallee et al., 2020), based on size or molecular weight, and association with mineral particles (Figure 12). Size and molecular weight are determinant for interactions with plant and microbes: only dissolved molecules are assimilable. Smaller molecules can also more easily be involved in chemical bonds with or adsorbed on reactive mineral surfaces, protecting them from enzymatic attacks, up to centuries or even millennia. Dissolved organic matter

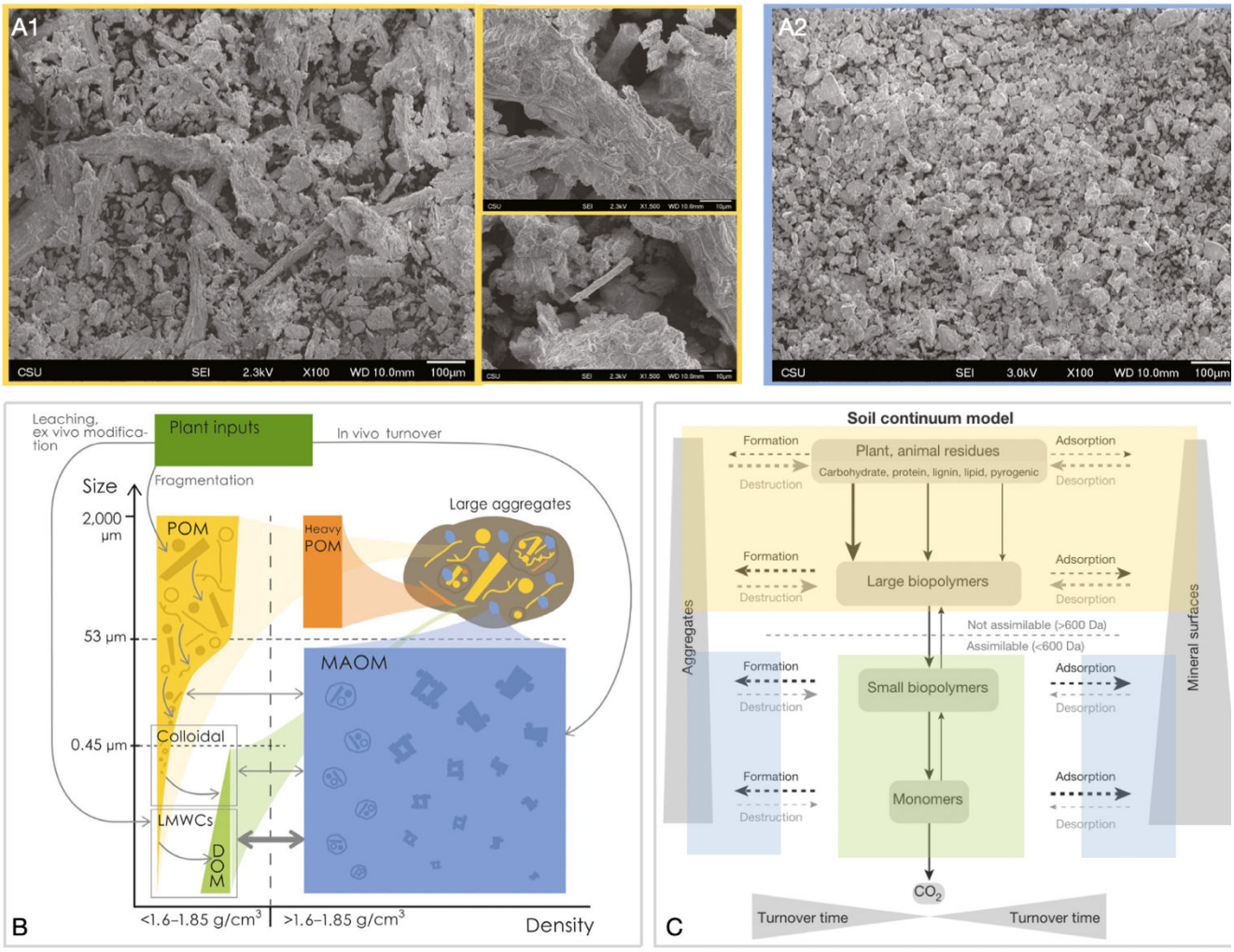


FIGURE 12 Modern conceptual frameworks for soil organic matter fractions

(A) Electronic microscopic images of particulate organic matter (POM, A1) and mineral associated organic matter (MAOM, A2) from a grassland soil (Lavallee et al., 2020). (B) The POM/MAOM conceptual framework proposed by Lavallee et al. (2020) and (C) The Soil Continuum Model proposed by Lehman and Kleber (2015), modified to include DOM, POM and MAOM compartments (green, yellow and blue coloured squares, respectively). In panel (A) continuous arrows represent biologically-driven transformations, while dotted arrows represent abiotic transfers.

(DOM) thus has the highest turnover rate. Both particulate organic matter (POM), originating from organisms' debris, and MAOM can also be protected though occlusion in macro- and microaggregate, respectively.

The soil continuum model (Figure 12C) is a good reminder that the boxes used by ecologists and modellers reflect a complex reality, and that one category can be heterogenous, both in its nature (e.g., origin of the residue, as in plant- or microbially-derived) and its interaction (e.g., type of association with mineral particles).

2.1.2 SOM transformation

Organic matter entering the soil system undergoes various transformations depending on its size, composition and localisation (Figure 13). Soluble molecules (DOM) from exudation, cellular lysis following predation/herbivory or leachates from litter decomposition can directly be absorbed by

microorganisms, and be oxidised for energy production (respiration) or used for biosynthesis of microbial biomass or exoenzymes. Both processes can lead to mineralisation, i.e. the liberation of inorganic molecules: energy production in aerobic conditions is associated with CO_2 emissions from microbial respiration, while both N or C can be mineralised during biomass formation. The balance between the stoichiometry of the substrate and that of the organism determines which element will be mineralised in larger quantity, with additional C respiration when N is limiting, and additional N mineralisation when N is in excess (Schimel & Weintraub, 2003). Other sources of DOM include transformation of soil organic matter through depolymerisation and solubilisation by exoenzymes, as well as MAOM desorption.

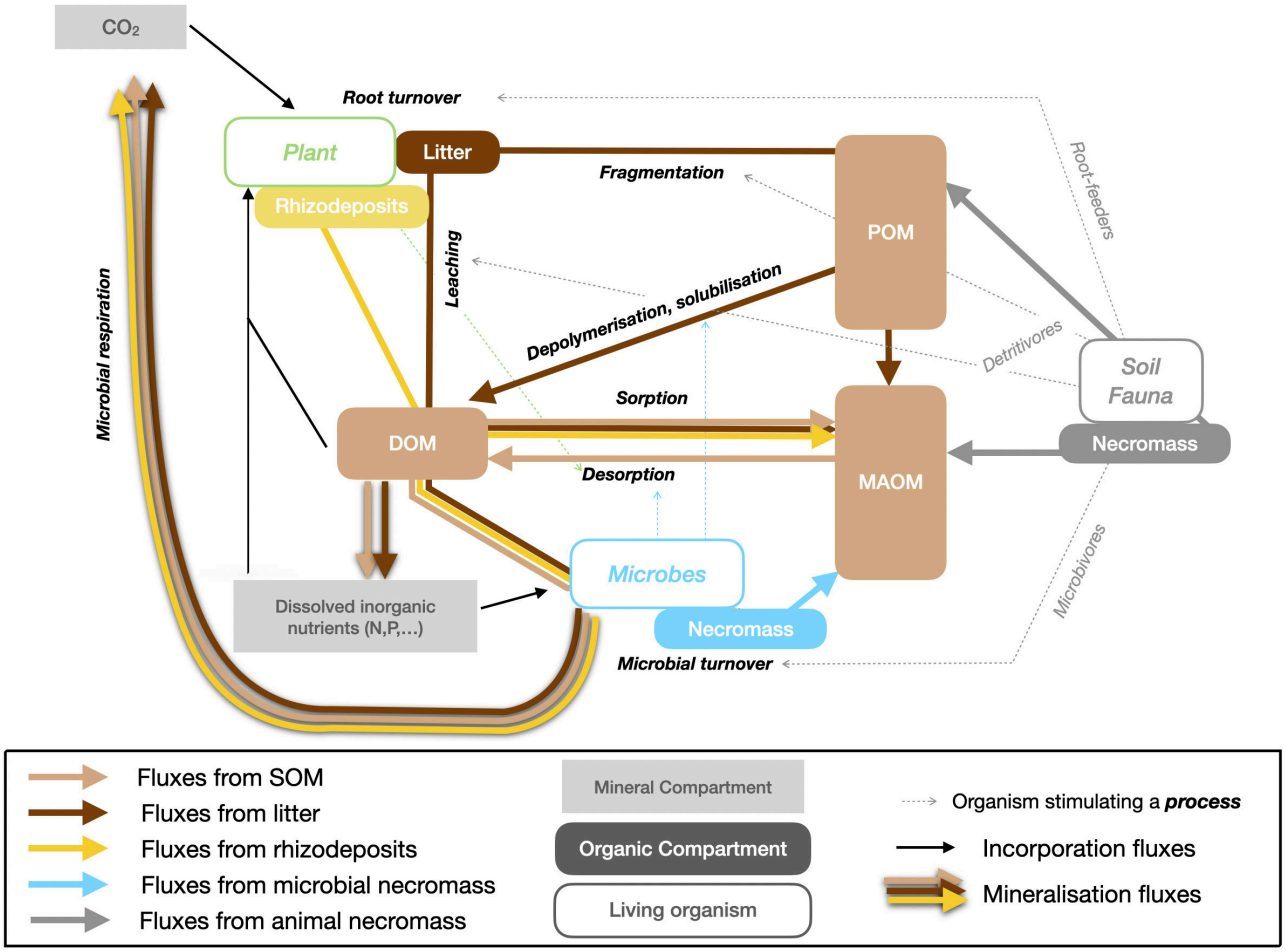


FIGURE 13 Overview of soil organic matter cycle, inspired by Ridgeway et al.(2024) and Wambsganss et al. (2025)

DOM: Dissolved Organic Matter; POM: Particulate Organic Matter; MAOM: Minerally Associated Organic Matter.

Litter fragmentation leading to POM is a step of litter decomposition primarily controlled by biotic factors (described under "transformation" in §1.2.1, highlighting that fragmentation is often concomitant with chemical modifications).

Death of living organisms leads to the formation of new SOM from their necromass, with a contribution to POM or MAOM depending on the organism size and its localisation. Estimations of microbial necromass contribution to MAOM formation range from 5 to 80% across studies, soil types, and

methodology, and often amounts to around 50% for grasslands (Whalen et al., 2022). Microbial turnover, controlled by microbivores, is therefore of particular importance for nitrogen cycle.

2.2. Focus on plant/microbes/microbivores interactions in the nitrogen cycle

We present in Figure 14 a simplified version of nitrogen cycle, focusing on some pivotal N species including amino acids, NH_3/NH_4^+, NO_3^- and N_2, thus ignoring numerous other forms[5] of N involved in intermediary transformations, with specific enzymes at each step, depending on the environmental conditions (aerobic/anaerobic).

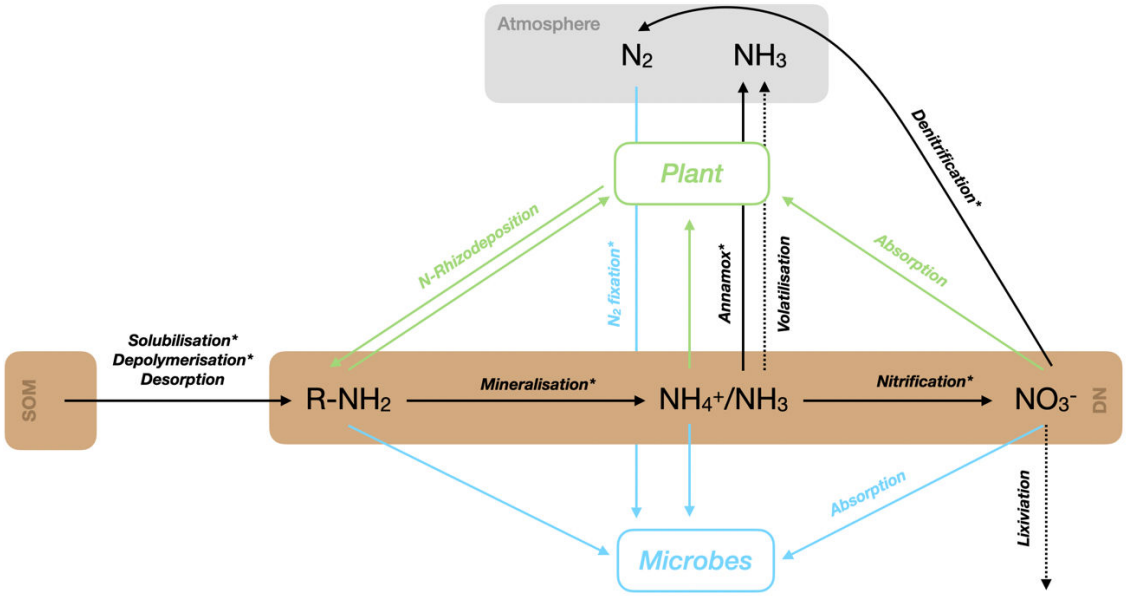


FIGURE 14 Simplified view of nitrogen cycling

Processes marked with an asterisk (*) are controlled by extracellular and/or intracellular microbial enzymes. SOM: soil organic matter. DN: dissolved nitrogen. R-NH2 represents amino-acids.

Notwithstanding, most microbial groups do not possess the enzymatic arsenal necessary to perform nitrification (i.e., the transformation of ammonium to nitrate), denitrification (i.e., the transformation of nitrates to N_2), or N_2-fixation, so groups who do represent a fundamental component of microbial functional diversity (Crowther et al., 2019, Table 1).

Ammonium (NH_4^+) and nitrates (NO_3^-) are mineral forms of nitrogen which can be absorbed by the roots (who often have a higher affinity for NH_4^+), alongside simple organic forms such as amino-acids ($R\text{-}NH_2$). The mineral forms are also the most sensitive to losses, through volatilisation (NH_4^+/NH_3) and lixiviation (NO_3^-). Plants and microbes thus compete for the same resource in the rhizosphere. It is established that

[5] The form of nitrogen most notably missing in this figure is nitrous oxide, a gaseous intermediary step of denitrification, which can also be lost to the atmosphere. It is a potent greenhouse gas, with a global warming potential of 273 (IPCC, 2023) which also participate to the thinning of the ozone layer (Ravishankara et al., 2009).

microbes, particularly bacteria, have higher intake capacities (Kuzyakov & Xu, 2013). However, they have distinct temporal niches: roots have a high lifespan, rhizosphere bacteria have a high turnover. Hence, when a root first explores a soil volume, the large mucilage around the apical meristem stimulates the microbial growth, but by the time the plant forms root hairs for nutrient absorption in that soil volume, microbial N recycling has started (Figure 15).

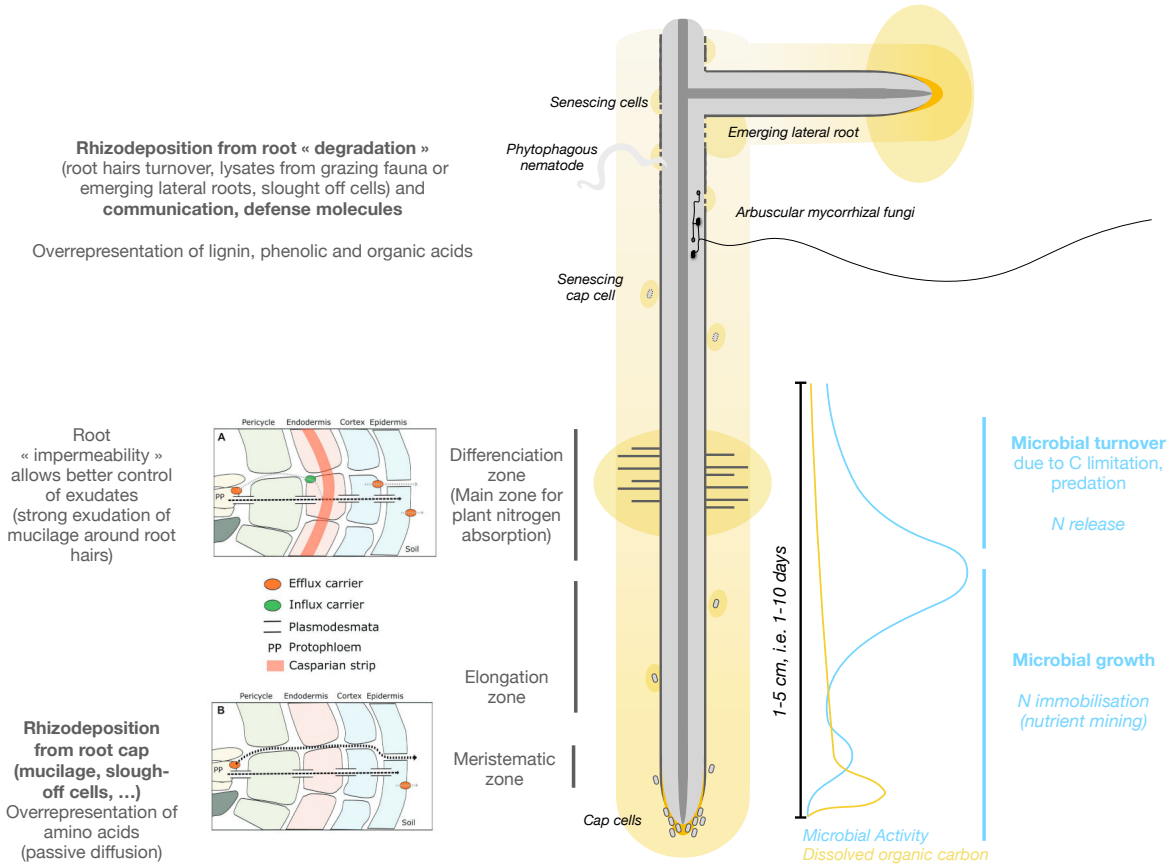


FIGURE 15 Microbial processes along the growing root in relation to rhizodeposition, based on Canarini et al., (2019); Dennis et al. (2010); Garcia Arredondo et al. (2024); Kuzyakov & Xu (2013)

Schematic representation of solute movement from phloem unloading (A, B), illustrating that plant control on rhizodeposition differs along the root are extracted from Canarini et al. (2019).

The total amount of nitrogen the plant will absorb through its root hairs is thus higher than what it would be without microbial growth, as microbial production of exoenzymes may have released additional nutrients (N or P) from SOM. This matter, which has already "cycled" through microbes will be made available to plants notably by the microbivores' excretion of NH_4^+, a process known as "the microbial loop" (Box 3, Bonkowski, 2004).

We have highlighted the importance of plant/soil biota interaction for soil organic matter. In the next section, we will see how different plants favour different mechanisms, according to their resource allocation strategies.

Box 3: The Microbial Loop

The presence of bacterial grazers, protists and bacterivorous nematodes leads to larger nutrient release (Trap et al., 2016), notably in the NH_4^+ form, which promotes plant growth. This is largely explained by their acceleration of SOM cycling processes, as revealed by accelerated N and P net mineralisation rates or higher microbial metabolic quotient (i.e., soil respiration per gram of microbial biomass), despite smaller microbial biomass in presence of bacterivores (Figure 16). This is due to grazing of senescent cells, promoting the growth of younger cells with higher metabolic activity thanks to nutrient release (direct effect).

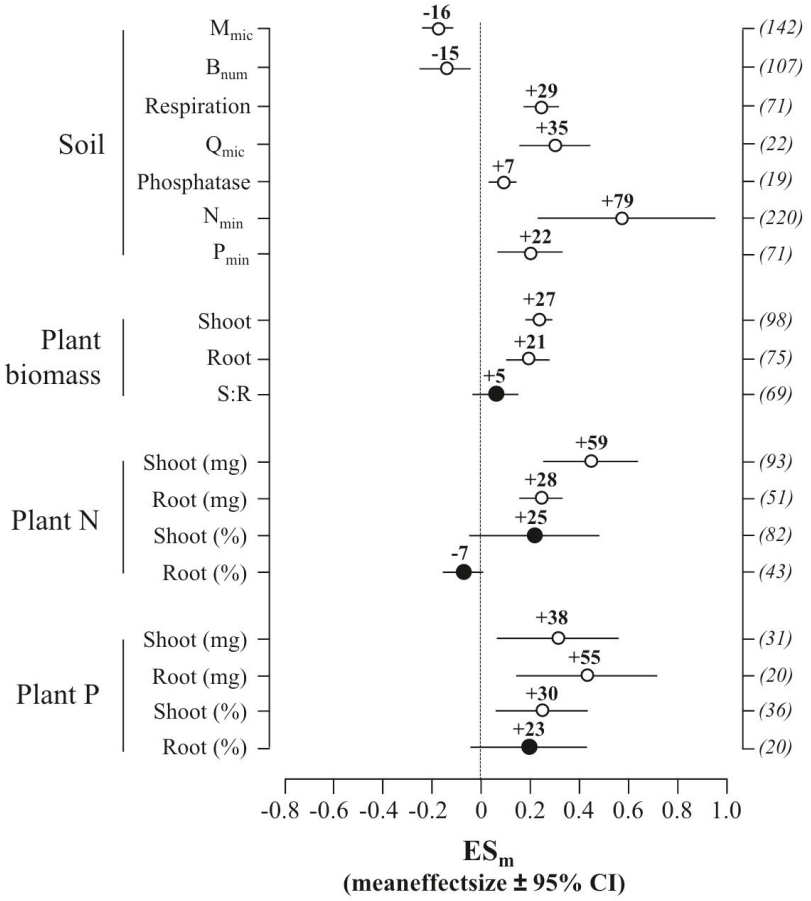


FIGURE 16 Mean effect size (ES_m) of bacterivores on ecosystem functions (Trap et al., 2016)

Bars indicate 95% confidence intervals (white point when significant, i.e. no intersection with 0, black otherwise). Bold numbers specify the ES_m expressed as % change compared to a control without bacterivore, italic numbers between brackets correspond to the number of observations.
M_{mic}: microbial biomass; B_{num}: bacterial number, Q_{mic}: microbial metabolic quotient;
N_{min}: net N mineralisation; P_{min}: net P mineralisation; S:R: shoot:root ratio

However, indirect pathways have also been demonstrated: bacterivores have been shown to enhance root growth while diminishing root nitrogen concentration (Figure 16), suggesting pathways independent of bacterivores' effect on nutrient availability. This could be associated with microbivores' implication in molecular signalling, for example to enhance root branching (Bonkowski, 2004). This may be associated to a strategy to promote higher plant inputs, fuelling higher microbial growth – that is, microbivore food.

3. Plant economic strategies

3.1. From Grime to the leaf economics spectrum and beyond

To address their needs of energy and nutrients across a wide variety of environments, plants have developed different life history strategies. Grime's "universal adaptative strategy theory" (1977) or "CSR framework", proposes that the competition for energy (light) and nutrients is mainly driven by plant relative growth rate (RGR), the faster growth of competitive [C] species allowing a better occupation (and thus exploitation) of nutrients and light patches. However, less competitive species can thrive in different environments through adaptation to stress (stress tolerant strategies [S]) or disturbance (ruderal strategy [R]).

DEFINITIONS FROM GRIME (1977)

COMPETITION	The tendency of neighbouring plants to use the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space.
STRESS	The external constraints limiting the rate of dry matter production of all or part of the vegetation.
PERTURBATION	The mechanisms limiting plant biomass by causing its destruction.

More recently, the opposition between resource conservation (stress tolerant, slow growing species) and resource acquisition (competitive and ruderal, fast growing species) have been further investigated in two dimensions and developed in the "plant economics space" (PES) theory (Reich, 2014; Weigelt et al., 2021; Wright et al., 2004).

This framework really focuses on how resource acquisition strategy is reflected by functional traits of organs related to resource acquisition (mainly leaves and fine roots), letting aside life history traits related to reproductive strategies.

Indeed, across all possible combinations of plant traits, only a few are realised (Díaz et al., 2016): some traits have to covary for the plant to have a viable strategy. The coordination of different functional traits has first been shown for six leaf traits (Wright et al., 2004): leaf mass per area (LMA), photosynthetic capacity, leaf nitrogen (LN), leaf phosphorus (LP), dark respiration rate and leaf lifespan. It revealed a "leaf economics spectrum", opposing species with fast metabolism expecting quick return on investment to species with lower metabolic rates and longer leaf life span, independent of a plant height.

DEFINITIONS FROM VIOLLE ET AL., 2007

TRAIT	Any morphological, physiological or phenological feature measurable at the individual level, from cell to the whole organism level, without reference to the environment or any other level of organisation.
ATTRIBUTE	Value or modality taken by a trait at a point of an environmental gradient.
FUNCTIONAL TRAIT	Any trait which impacts fitness indirectly via its effects on growth, reproduction and survival.
RESPONSE TRAIT	Any trait the attribute of which varies in response to changes in environmental conditions.
EFFECT TRAIT	Any trait which reflects the effects of a plant on environmental conditions, community or ecosystem properties.

This framework has then been extended at the whole plant scale (Reich, 2014): in order for a strategy to successfully influence fitness, it must be consistent across **organs** and *resources*. For **leaves** to be competitive for *light* (and *carbon*) acquisition and support fast growth, **roots** must be acquisitive to supply enough *nutrients* to produce the N-rich enzymes needed for photosynthesis, as well as enough *water* to sustain evapotranspiration, which drives transport of nutrients to the leaves through the **stem**.

However, roots traits do not consistently align with a single fast-slow growth trade-off (Kramer-Walter et al., 2016; Reich, 2014; M. Zhou et al., 2018). For instance, specific root length (SRL) reflects soil volume exploration per unit mass and was considered analogous to specific leaf area (SLA), thus representative of the acquisitive strategy. Yet, it was regularly found to vary independently of the fast/slow gradient formed by roots and leaves nitrogen content and structure-related traits (dry matter content, tissue density). Root traits are not the only determinant of soil volume exploration efficiency (which plays a tremendous part in nutrient acquisition efficiency[6]): more than 85% of plant species form mycorrhizal associations with fungi, exchanging carbon against nutrients (see Box 4: Mycorrhization). Accounting for mycorrhizal hyphae to estimate the area, the exploration efficiency rises from a factor 2 to 6, and reveals that bigger roots with a high mycorrhization rate can be associated with high resource acquisition despite low SRL (McCormack & Iversen, 2019).

This has led the scientific community to consider a plant economics *space* including two economic independent dimensions (Bergmann et al., 2020; Weigelt et al., 2021) rather than the unidimensional plant economics *spectrum*, still independent of plant size.

[6] Other components of nutrient acquisition efficiency include affinity for the elemental species available in the soil solution and maximum net uptake capacity which tend to align with the fast strategy, (Freschet, Roumet, et al., 2021), or foraging precision (Stiblíková et al., 2023) which are beyond the scope of this study.

The three dimensions include (Figure 17):

- the **conservation gradient**, or FAST-SLOW GRADIENT, including the leaf economics spectrum, reflecting the trade-off between high metabolic activity and long life-span;
- the **size gradient**, expending for instance Díaz et al. (2016)'s height dimension with rooting depth trade-off, which is beyond the scope of this study, as we will focus on herbaceous grassland species;
- the **cooperation gradient** or **belowground morphological efficiency gradient**, representing the trade-off regarding exploration of the soil volume, between a "do-it-yourself strategy" when a plant invests in its own efficient root system and an "externalisation strategy", when a plant relies on a mycorrhizal partner for soil foraging (Box 2). Thus, we will hereafter name it the EXPLORATION GRADIENT.

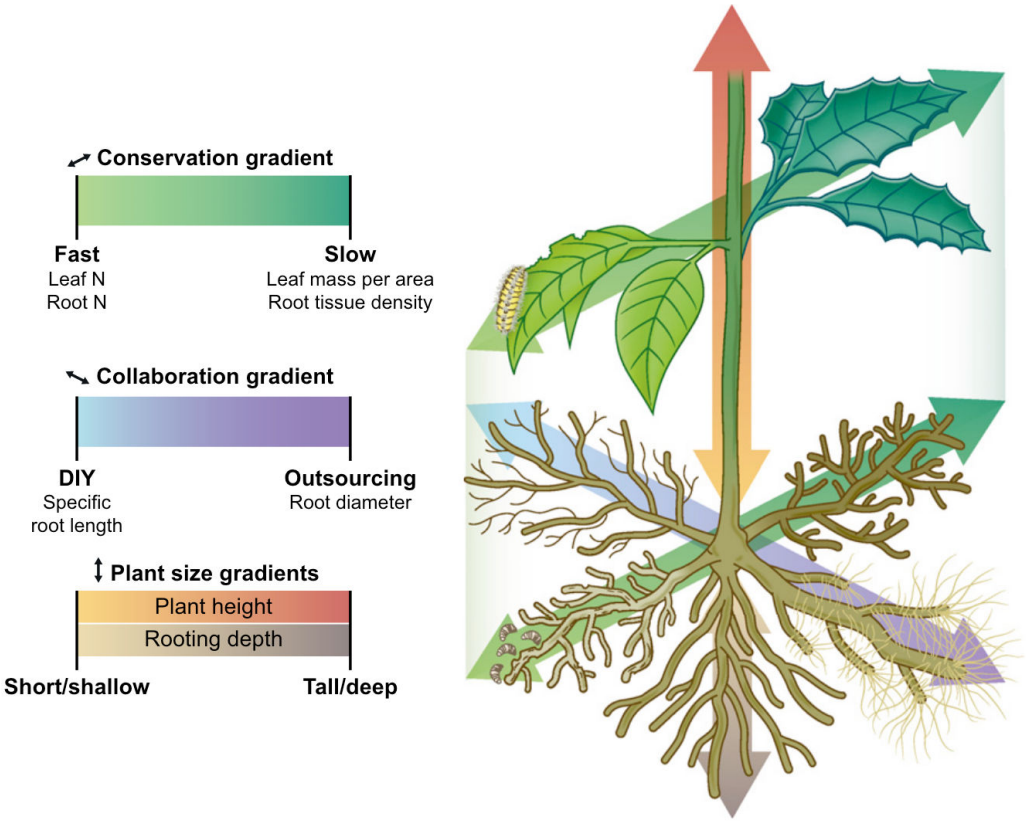


FIGURE 17 The conceptual framework of the Plant Economics Space (PES), following Weigelt et al., (2021).

Traits indicated at one gradient extremity are the traits where high values are an expected attribute of species featuring this strategy.

Each gradient is reflected by specific functional traits, beyond those presented in the Figure 17. For example, beside high leaf mass per area and higher root tissue density, conservative species are expected to have high dry matter content, while high SLA is supposed to be characteristic of acquisitive species.

Aboveground physiological traits have been included since the beginning in the leaf economics spectrum with maximum photosynthetic rate and leaf respiration aligning with the acquisitive end of the gradient

(Reich, 2014; Wright et al., 2004). Contrarily, belowground physiological traits such as rhizodeposition, root respiration and mycorrhizal colonisation have mostly lacked this consideration, notably because they are harder to measure: the largest meta-analyses on the plant economics space (Weigelt et al., 2021) is based only on morpho-chemical traits, though Bergmann et al. (2020) include the proportion of AMF colonisation for a smaller set of species. While the relationships between root traits and root respiration (Han & Zhu, 2021) or exudation (Guyonnet, Cantarel, et al., 2018; Williams et al., 2022) have already been explored, there are very few studies including more than one physiological root trait (Henneron, Cros, et al., 2020; Sun et al., 2021).

Box 4: Mycorrhization

Arbuscular mycorrhiza have likely played a pivotal role in plant evolution, supporting the colonisation of terrestrial environments. The implication of AM fungi in phosphorus (P) acquisition is well documented, as they provide their host with P from beyond the root depletion zone. Contrary to some EcM fungi, they do not possess saprotrophic capacities and as such, they have been considered to play a minor role in nitrogen (N) cycling. However, their influence might be underestimated, as they represent a major sink for nitrogen (Hodge & Fitter, 2010) and, like EcM, they have the ability to colonise litter, promote its decomposition and absorb N from this decomposing organic matter, though only an inorganic form (Hodge et al., 2001).

Mycorrhization capacity has been repeatedly lost (but also gained) during the evolution, mostly in plant species adapted to oligotrophic, aquatic or disturbed environments, and nutritional specialists such as carnivores (Brundrett & Tedersoo, 2018). This loss has also been documented in some terrestrial herbaceous families such as Chenopodiaceae, Carophyllaceae, and Brassicaceae (Cosme et al., 2018), revealing alternate viable resource acquisition strategies. These non-host species can however show signs of rudimentary colonisation by host-supported fungi, to the detriment of the non-host (Cosme et al., 2018) and highlighting that this "long-term intimate relationship" might not always benefit all partners. Indeed, even for host plants, it has been shown that mycorrhization could range from mutualism to parasitism, depending on environmental conditions and the AM fungi species (Hoeksema et al., 2010).

In their recent review of the application of the root economics framework to fine root traits research, Matthus et al. (2025) underlined the need for further investigation of other traits, including more physiological traits like rhizodeposition, notably to better establish the limits of this framework. They also highlighted the existing support for the link between the root economics space and ecosystem functioning, though we still lack generalised hypotheses, especially regarding the exploration gradient. In the next section, we review the evidence of the linkages between root traits and ecosystem functioning, or to phrase it differently, which root traits are the belowground effect traits.

3.2. Belowground effect traits for understanding SOM cycling

Plant belowground economics strategies have been increasingly linked to soil organic matter cycling in the past few years. Indeed, architectural traits condition the localisation of C inputs (either from root turnover or from rhizodeposits) and of nutrient-depletion zones in the soil volume, while physiological traits (root life span, growth rate) determine the quantity of inputs, and chemical traits (C:N, lignin content) their quality (Bardgett et al., 2014; Table 2).

The dominant idea is that acquisitive species are associated with faster carbon and nutrient cycling rates (Henneron, Cros, et al., 2020; Henneron, Kardol, et al., 2020; Legay et al., 2016; Wardle, 2004). This effect is likely mediated by plant effect on microbial communities, through both direct living roots trait influence (Figure 18), and indirect impact of economics strategy on litter properties (Freschet et al., 2012; Wambsganss et al., 2025).

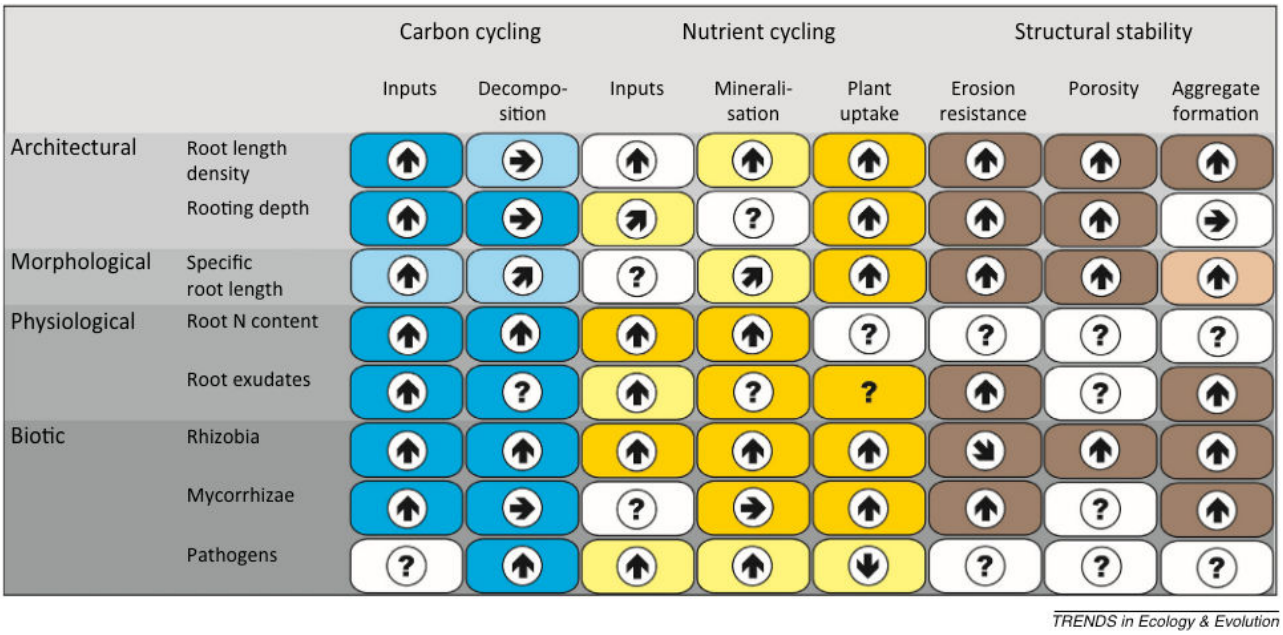
Acquisitive species have been shown to promote bacteria over fungi, leading to lower *f:b* ratios (Grigulis et al., 2013; Legay et al., 2014; X. Wan et al., 2021), and higher enzymatic activities (Grigulis et al., 2013; Han et al., 2023), though there are contrasting results (X. Wan et al., 2022).

Acquisitive species have litter of higher quality, with high decomposition rates while conservative species feature slower decomposition rates. This "economics spectrum of litter decomposability" is primarily explained by structure-related traits (Freschet et al., 2012), i.e. higher carbon, lignin and dry matter content. Conservative species also have tissues with higher chemical recalcitrance, leading to short term carbon accumulation, while acquisitive species promote the formation of stable mineral associated organic matter (Poirier et al., 2018).

If nutrient-related traits (e.g., N, P, and phenols content) were found to have more variable influence on decomposition rate across organs, C:N:P stoichiometry of root, litter and SOM are increasingly recognised as regulators of the direction and magnitude of priming effect (Carrillo et al., 2017; Chao et al., 2019; Dijkstra et al., 2013).

TABLE 2 – Root traits and their potential impact on three soil processes (Bardgett et al., 2014)

Upward/downward/horizontal pointing arrow indicates predominantly positive/negative/absent effect, respectively, while question mark indicates insufficient evidence. Colouring shade indicates the degree of uncertainty (white = knowledge gaps).



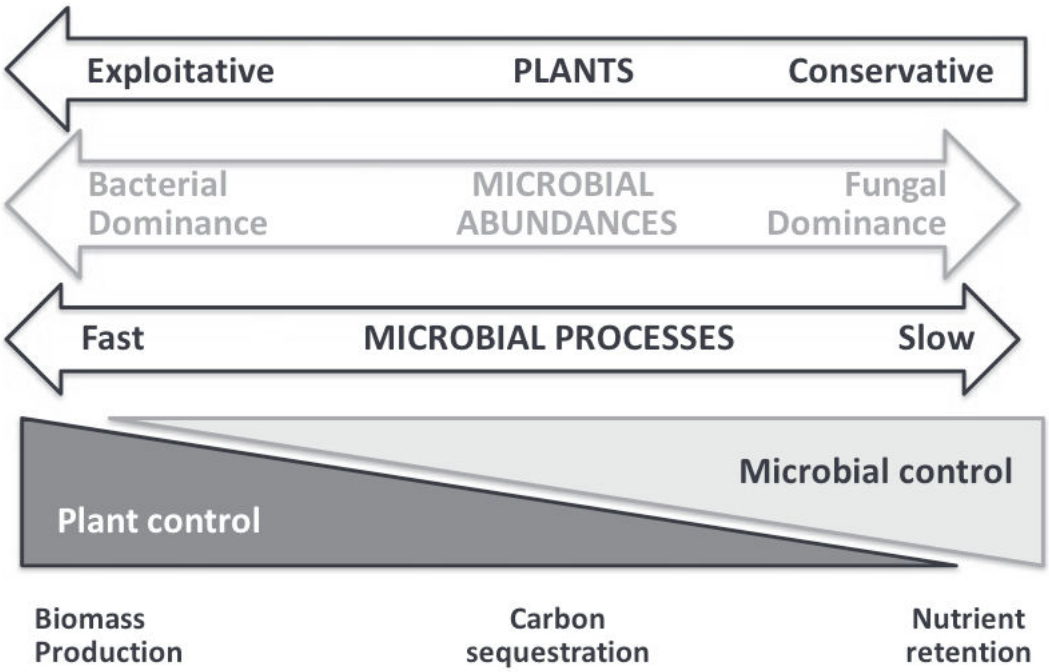


FIGURE 18 Schematic overview of simultaneous variations in plant functional strategies, microbial functional composition and activities, and ecosystem processes and services in a mountain grassland (Grigulis et al., 2013)

4. Scope of the study

Cutting a long story short, plant-derived organic matter, litter and rhizodeposition are essential components of ecosystem functioning: from basal resources in soil food webs to key mediators of SOM cycling processes, either directly or indirectly, their influence is well recognised. Plant economic strategies, i.e. functional trait syndromes coherent across organs, control this influence by affecting quantity and quality of plant-derived organic matter inputs, with long-term consequences for ecosystem functioning. In brief, plant economic strategies can be described by two independent traits gradients representing trade-offs concerning plant resource acquisition: the fast/slow gradient opposes acquisitive species (fast growth, high nitrogen content and low dry matter content, high quality litter) to conservative species (opposite traits syndrome), while the exploration gradient opposes outsourcing species (high root diameter, root cortex fraction, and low specific root length) to "do-it-yourself" species (opposite traits syndrome).

Yet, if the impact of litter quantity and quality, as well as of various root traits are well-documented, studies on rhizodeposition and root exudates in the plant economics space are still too rare, considering their importance for rhizosphere priming and soil food webs. More, while rhizodeposits are increasingly recognised as a key basal resource, fuelling the fast rhizosphere channel, its relative importance compared to litter has yet to be quantified. Finally, the economics space of litter decomposition is too often studied in controlled conditions without plants, even though plant strategies' impact on ecosystem functioning is likely to be mediated by plant uptake as well. Notably, there are no studies investigating how the exploration gradient affects litter decomposition and litter-derived N recycling in the plant/microbe/soil system.

4.1. Objectives and hypotheses

In this manuscript, we will investigate plant/soil biota interactions across 15 grassland species through two plant-derived resources: litter and rhizodeposition (Figure 21).

We will first explore (Chapter 1) **HOW RHIZODEPOSITION FITS IN THE PLANT ECONOMICS SPACE**, along with two other physiological traits (root respiration and AMF colonisation rate), and **HOW THIS SHAPES INTERACTIONS WITH THE MICROBIAL COMMUNITY**.

More precisely, we hypothesize (H1.1), that:

- AMF colonisation aligns with the "outsourcing" strategy,
- Root respiration aligns with the "acquisitive" strategy,
- Rhizodeposition shows positive relationship with both outsourcing and acquisitive strategy.

We also expect (H1.2) the microbial community to respond to plant economic strategy, the outsourcing species promoting AMF over other microbial groups, while the acquisitive species promote Gram– bacteria.

Then, we will evaluate the **RELATIVE IMPORTANCE OF LITTER AND RHIZODEPOSITION FOR SOIL FOOD WEB FUNCTIONING** and assess whether plant economic strategies influence the food web energetics through living plant traits and litter properties (Chapter 2).

More precisely, we hypothesize that (H2.1) rhizodeposition and litter both support energy channels of the same magnitude, and the presence of each resource independently fuels higher energy fluxes in soil food webs (i.e., additivity of basal resources), and that (H2.2) the relative importance of fungal and bacterial channels varies with the resource type, with stronger fungal channel in presence of litter and stronger bacterial channel in presence of rhizodeposition. We also expect (H2.3) acquisitive plant species to support higher fluxes.

Finally, we will study **HOW PLANT ECONOMIC STRATEGIES AFFECT LITTER NITROGEN RECYCLING**, particularly, plant and microbe acquisition of litter-derived nitrogen (Chapter 3).

More precisely, we hypothesize that (H3.1) patterns of litter derived nitrogen recovery in microbial biomass, above- and belowground plant parts can be explained by plant economic strategy, with higher plant recovery for acquisitive species, and that (H3.2) this effect is mediated by plant strategy's influence on microbial activity (net nitrogen mineralisation, soil respiration). We also expect (H3.3) microbivory to be determinant in explaining litter derived nitrogen recovery in plants, because of the microbial loop.

To close this introduction, Figure 21 (p. 40) displays an overview of the overarching question for each chapter and the core hypotheses.

4.2. Overview of the experimental design[7]

In order to test these hypotheses, we set up a common garden experiment crossing litter addition and living plants in monospecific conditions for 15 grassland species (Table 3), using a dual $^{15}N/^{13}C$ labelling (Figure 19).

[7] Due to the structure of the manuscript, this section is partly redundant with the materials and methods of the articles. It aims at giving an overview of the experimental design, accompanied by additional details (for example, description of the site of soil collection).

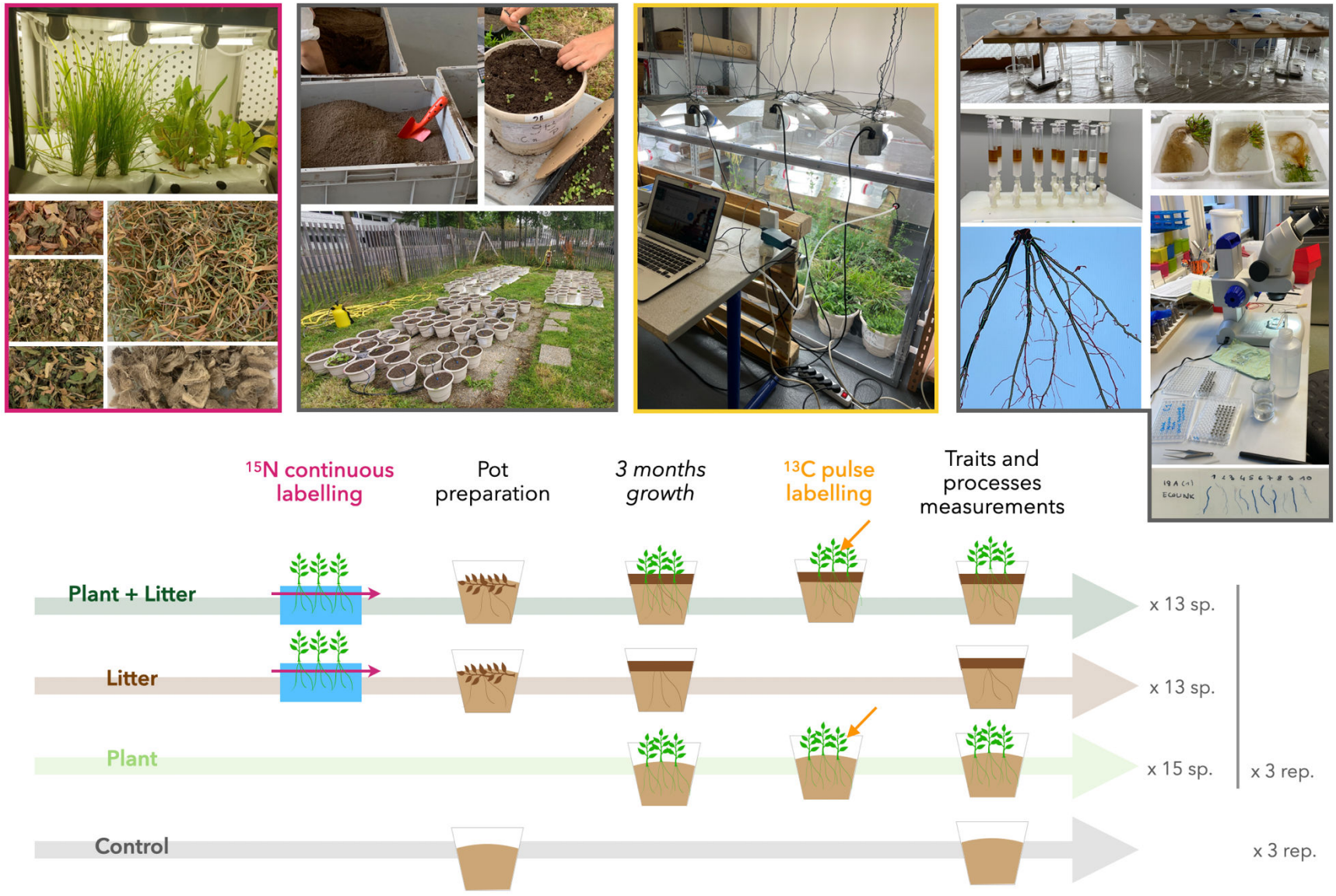


FIGURE 19 Overview of the experimental design

The "traits and processes measurements" box shows KCl extraction, PLFA extraction, roots system prepared to be scan, root scan, preparation of fauna samples for IRMS analysis and root fragments coloured for assessment of mycorrhizal colonisation. sp.: Species; rep.: replicates.

TABLE 3 – Overview of plant traits in our experiment

Values reported are mean ± 1.96 · sd (95% confidence interval for the distribution).

Species and abbreviation		***Funct-ional Group***	***Family***	***Whole plant***	***Leaf traits***					***Belowground traits***				
				AGR	*SLA*	*LNC*	*LDMC*	*SRL*	*RMD*	*RNC*	*RDMC*	*RhSoil*	*%AMF*
				mg day^{-1}	*cm^2 · g root^{-1}*	*%*	*%*	*cm · mg root^{-1}*	*mm*	*%*	*%*	*nmolC· g soil^{-1}*	*%*
Nardus stricta (L., 1753)	N.s.	Graminoid	Poaceae	4.0 ± 3	175.3 ± 26.4	4.05 ± 1.65	30.2 ± 7.2	9.23 ± 5.59	2.93 ± 1.27	1.46 ± 0.48	14.2 ± 3.4	49.3 ± 23.9	17.8 ± 27.5
Festuca ovina (L., 1753)	F.o.	Graminoid	Poaceae	16.8 ± 7.5	153.9 ± 51.4	3.19 ± 1.34	25.5 ± 3.8	20.5 ± 4.5	1.77 ± 0.24	1.43 ± 0.28	13.2 ± 5.7	35.2 ± 26.5	21.6 ± 32.5
Dactylis glomerata (L., 1753)	D.g.	Graminoid	Poaceae	16.3 ± 8.1	301.4 ± 67.8	3.68 ± 1.18	21.4 ± 3.6	24.6 ± 11.8	1.72 ± 0.2	1.21 ± 0.44	13.9 ± 4.4	29.3 ± 13.8	15.1 ± 24.8
Holcus lanatus (L., 1753)	H.l.	Graminoid	Poaceae	21 ± 10.9	366.3 ± 39.1	2.79 ± 0.67	21.0 ± 1.7	31.7 ± 18.6	1.55 ± 0.21	1.08 ± 0.33	14.4 ± 5.6	38.3 ± 58.1	14.8 ± 32.9
Anthoxantum odoratum (L., 1753)	A.o.	Graminoid	Poaceae	25.9 ± 13.1	257.0 ± 19.3	2.56 ± 1.02	23.9 ± 2.3	24.0 ± 7.1	1.72 ± 0.29	1.00 ± 0.25	13.2 ± 4.1	59.9 ± 90.7	9.2 ± 15.6
Campanula rotundifolia (L., 1753)	C.r.	Forb	Campanulaceae	4.84 ± 3.8	349.6 ± 65.5	5.63 ± 1.48	17.7 ± 3.3	34.3 ± 33.7	1.75 ± 0.27	2.65 ± 0.18	9.1 ± 5.6	18.9 ± 25.4	5.5 ± 8.4
Galium verum (L., 1753)	G.v.	Forb	Rubiaceae	10.6 ± 7.7	260.0 ± 59.7	4.07 ± 1.77	19.4 ± 3.3	23.6 ± 10.2	1.69 ± 0.19	1.88 ± 0.22	13.3 ± 1.5	36.1 ± 17.7	4.9 ± 9.6
Plantago lanceolata (L., 1753)	P.l.	Forb	Plantaginaceae	18.1 ± 5.6	243.8 ± 92.5	3.17 ± 1.21	13.2 ± 2.6	14.9 ± 5.1	2.47 ± 0.61	1.35 ± 0.43	11.8 ± 2.9	36.6 ± 32.4	27.9 ± 44
Centaurea nigra (L., 1753)	C.n.	Forb	Asteraceae	22.6 ± 6.4	207.2 ± 45.6	2.80 ± 1.07	16.3 ± 2.7	7.04 ± 3.05	2.86 ± 0.72	1.04 ± 0.26	15.4 ± 2.2	29.6 ± 26.3	34.9 ± 19.6
Rumex acetosa (L., 1753)	R.a.	Forb	Polygonaceae	29.1 ± 9.8	305.0 ± 86.5	3.38 ± 1.59	10.2 ± 0.8	7.33 ± 3.91	2.52 ± 1.00	1.08 ± 0.42	20.4 ± 8.8	65.3 ± 37.6	0 ± 0
Trifolium repens (L., 1753)	T.r.	Legume	Fabaceae	15.1 ± 14.2	343.0 ± 76.5	5.27 ± 1.57	15.7 ± 3.0	9.41 ± 4.46	3.08 ± 0.22	3.26 ± 0.74	11.4 ± 5.6	30.6 ± 32.2	25.0 ± 36.1
Trifolium pratense (L., 1753)	T.p.	Legume	Fabaceae	20.0 ± 9.9	320.4 ± 40.4	4.98 ± 1.62	20.7 ± 1.5	10.7 ± 4.7	2.80 ± 0.18	3.01 ± 1.09	12.9 ± 5.3	56.4 ± 44.9	21.2 ± 24
Melilotus albus (Medik, 1787)	M.a.	Legume	Fabaceae	18.3 ± 9.9	213.7 ± 58.4	3.87 ± 1.11	19.0 ± 2.4	6.62 ± 5.72	3.46 ± 0.85	3.40 ± 0.97	14.8 ± 8.2	92.9 ± 126.6	25.3 ± 36.9
Medicago sativa (L., 1753)	M.s.	Legume	Fabaceae	21.5 ± 8.4	279.5 ± 41.1	4.38 ± 1.61	20.9 ± 1.5	6.37 ± 3.89	3.34 ± 0.21	2.90 ± 0.76	15.6 ± 8.1	101.9 ± 125.8	8.6 ± 14.3
Lotus corniculatus (L., 1753)	L.c.	Legume	Fabaceae	22.3 ± 8.8	219.7 ± 40.9	3.64 ± 1.27	18.7 ± 2.9	5.32 ± 3.64	3.76 ± 0.59	2.92 ± 0.78	14.0 ± 6.6	95.9 ± 104	29.0 ± 26.8

Box 5: Tracking elemental fluxes with isotopic labelling

Stable isotope labelling consists in exposing a system to a tracer, enriched or depleted in the scarce heavy isotope compared to its natural concentration. In our case, the isotopes of interest are ^{13}C (natural abundance: 1.06 atom%) and ^{15}N (natural abundance: 0.4 atom%), which have an abundance of 10% in our tracers.

Follow up of the tracer in various compartment will be expressed either as enrichment (ppm) or in proportion of recovered tracer (%, ppm). **ENRICHMENT** is calculated as the difference between the tracer atom% and an unlabelled baseline atom% (Slater et al., 2001). **PROPORTION OF THE RECOVERED TRACER** is calculated based on a tracer mass balance approach (Rasmussen, 2011), either based on the tracer input quantity (thus including losses, like for ^{15}N mass balance in Chapter 3) or the quantity of tracer recovered across all compartment of interest (like for ^{13}C mass balance across microbial groups, in Chapter 2, Supplementary materials).

Description of soil collection site

The soil was collected from the first 20 cm of a loamy permanent (> 15 years) urban mesophilic grassland at 49°28'28.3"N 1°04'17.6"E in Mont-Saint-Aignan (France), with a pH of 6-6.5 (Figure 20). The soil was sieved at 5 mm for homogenisation, and the removal of roots and macrofauna. Pots were filled at a volumetric mass of 0.8 $g \cdot cm^{-3}$.

Production of ^{15}N labelled litter

^{15}N labelled litter was produced in hydroponic conditions, and senesced by progressively decreasing the watering frequency over 2-3 weeks. 0.7 g · pot-1 of root litter, incorporated in the first 7 cm and 1.5 g · pot-1 of leaf litter deposed on the surface. Quantities were calculated to be coherent with living plant density. Because litter production of *Campanula rotundifolia* and *Nardus stricta* was insufficient, these two species are excluded from the treatment including litter.

Across this manuscript, we will use the word **TREATMENT** to refer to the combination of litter and living plants presence/absence – amounting to four treatments: control (C), litter-only (L), plant-only (Pl) and plant+litter (Pl+L). The word **MODALITY** will refer to the intersection of a treatment with a given plant species.

Growth

Plants were grown for three months in an experimental garden, at a density of 7 individuals per pot (20 000 $ind \cdot m^{-2}$), were installed in three blocks, with one replicate of each modality per block. Block corresponds to placement in the experimental garden and week of harvest.

^{13}C pulse labelling

^{13}C pulse-labelling was conducted at the end of the experiment. All pots from treatments with plants (Pl, Pl+L) of one block were labelled in one batch, i.e. inside the same labelling chamber. Plants were labelled during 6 hours daily on two consecutive days, to allow the tracer to be incorporated in microbial groups and microarthropods.

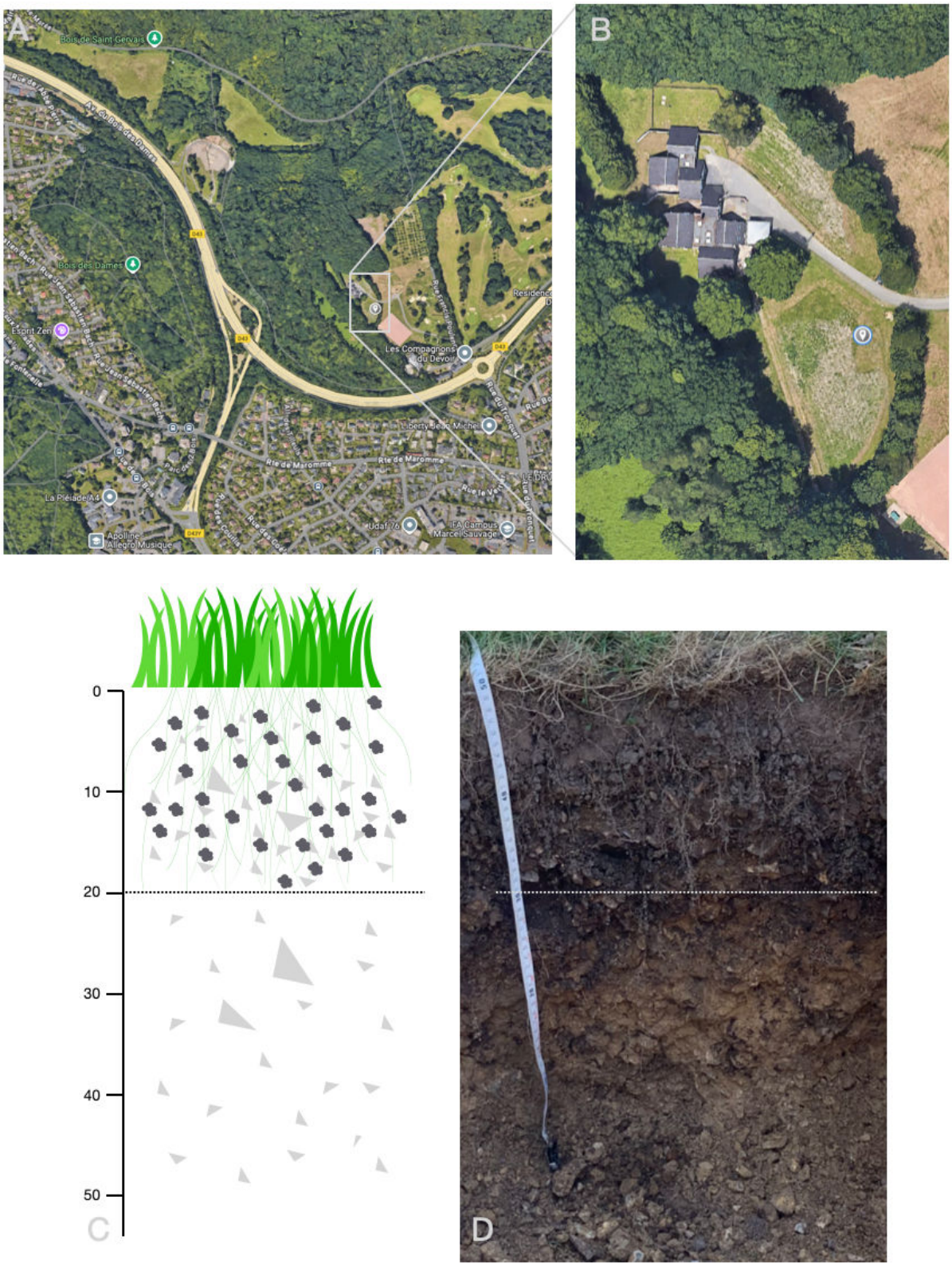


FIGURE 20 Overview of the soil used for the experiment

Localisation of the grassland (A), with a zoom on the sampling zone (B), schematic (C) and photographic (D) view of the soil profile. Triangles represent coarse elements (that were up to 10 cm big). Point line indicates the limit of sampling depth.

Harvest and measurements

48 hours after the start of the labelling, pots were harvested, to destructively characterise: microarthropods and nematodes communities, plant traits (scanning, chemical analyses, and root respiration measurements), microbial communities (fumigation-extraction, PLFAs extraction) and soil C & N cycling (24h incubation for soil respiration, 5 days for nitrogen mineralisation). Isotopic analyses of the following compartments were performed: above-ground biomass, belowground biomass, SOM, SOM respiration (from the 24h incubation), microbial biomass (fumigation-extraction), microbial PLFAs, and microarthropods. Rhizodeposition was defined as the quantity of tracer recovered outside the plant (microbial biomass and soil respiration), corrected by the intensity of labelling (Box 6).

Isotopic measurements are at the core of this manuscript, and are developed under different angles in each chapter. The first chapter explores the relative enrichment of microbial groups, the second uses the ^{13}C mass balance in PLFAs to assess preference parameters of microbial groups for soil food web modelling (Box 7) and the last chapter is based on the ^{15}N mass balance.

Box 6: The challenging measure of rhizodeposition

The term "rhizodeposition" was coined by Shamoot et al. in their 1968 paper[8], to describe the 10-30% plant-derived soil organic carbon they found, using $^{14}CO_2$ continuous labelling of eight crop species. CO_2 continuous labelling with radioisotopes or stable isotopes remains one of the predominant methods used to study rhizodeposition quantitatively (Oburger & Jones, 2018). Alternative methods focus on root exudates sampling, mostly performed in hydroponics.

There are, however, debates as to what should be considered rhizodeposition, especially whether or not root turnover and resource allocation to root symbionts should be included. For example, Rasmussen (2011) argues that the term should be restricted to processes related to the living roots. Actually, the definition used is often constrained by the methodology used for measurement: with long-term continuous labelling, root turnover is necessarily included, while with pulse labelling, it is usually excluded[9].

DEFINITIONS FROM OBURGER & JONES (2018), ADAPTED FOR THIS MANUSCRIPT

RHIZODEPOSITION	All of the organic carbon derived from roots that is lost into the soil. This includes compounds lost from live roots (e.g. root exudates, root cap cells, border cells), root symbionts (mycorrhizas, N_2 fixing bacteria, dark septate fungi) ~~and also compounds lost from senescing and dead roots (i.e. root turnover)~~.
ROOT EXUDATION	Soluble organic compounds lost from the surface of living root cells into the soil, including low molecular weight (< 1000 Da; e.g. sugars, organic acids, phenolics, vitamins) and high molecular weight (> 1000 Da; e.g. enzymes, mucilage).

To exclude carbon allocation to root symbionts and other microbial mutualists, one needs to be sure that the collected molecules are produced by the plant and not by microorganisms closely associated to it. This is a difficulty shared both by labelling experiments and exudate collection techniques in non-sterile conditions.

In this manuscript, because we used $^{13}CO_2$ pulse labelling with a follow-up period of two days, we will use a definition excluding root turnover, but including resource allocation to root symbionts. This is particularly relevant for our research questions, as we are interested in how rhizodeposition is related to acquisition strategies at the individual scale, for example the trade-off between investment in a plant's own foraging system compared to the investment in mycorrhizal symbiosis, and not on the different pathways of SOM formation from root.

It will be expressed as a quantity of carbon per gram soil or per gram root. The latter will be termed **SPECIFIC RHIZODEPOSITION**. We will use exudation/rhizodeposition **RATE** to refer to studies who express this quantity per unit time, which is not our case.

[8] I think – I didn't find an older occurrence of the term with a Google Scholar of Web of Science search.
[9] Though it depends of the time between labelling and sampling, as root lifespan of grassland species range from several weeks to several months (Van Der Krift & Berendse, 2002).

Box 7: Soil food web modelling

Stable isotope probing, but also the study of natural fractionation processes across trophic levels, have been essential in resolving the question of who eats what in soil food webs. Tremendous progress has been made in the past years by coupling this with other methodologies, for example gut content analysis. A recent synthesis by Potapov et al. (2022) gives an overview of soil fauna preferences, but no such synthesis exists for microbial groups, so we assessed preferences based on the enrichment of PLFAs (^{13}C) and microbial biomass (^{15}N).

Elucidating the interactions is necessary for a better understanding of soil food webs, but is not enough to gain a quantitative understanding of energy and nutrient fluxes. Various modelling approaches exist, but they partly rely on parameters that are difficult to measure, like death rate of each trophic group.

An approach of energy flux calculation focusing on metabolic needs and assimilation efficiencies has been thoroughly described by Jochum et al. (2021) and made accessible in the R package "fluxweb" by Gauzens et al. (2019). As metabolic demand can be approximated by respiration, it is much easier to find data in the literature or to use one's own measurements as a parameter of the model (for example, microbial respiration). Animals metabolic rate can also be estimated from their individual mass thanks to the allometric equation $X = i_0 M^a e^{-\frac{E}{kT}}$ (Downs et al., 2008), where M is the body mass (mg), E is the activation energy (eV), T is the temperature, k is Boltzmann's constant, and i_0 and a are constants, which can be specific to functional or taxonomic group (Ehnes et al., 2011).

In a nutshell, a flux F between a resource node i and its only consumer j is calculated as $F_{ij} = \frac{1}{e} \cdot (X + L)$, where e is the assimilation efficiency (specific to either this particular interaction, to the consumer or to the resource), X is the metabolic demand of the node, and L the loss to consumption. For top predators, $L = 0$, while $X = 0$ for basal resources.

In a network where a node i is implicated in several trophic interactions, its losses L_i are defined by the following equation:

$$L_i = X_i + \sum_j F_{ij}$$

where F_{ij} is the flux from node i to is consumer node j.

Its gains G_i are defined by:

$$G_i = \sum_j F_{ji} e_{ij}$$

where e_{ij} can depend on i, j, or both.

The package "fluxweb" solves the matrix F by computing the sum of ingoing fluxes to each node assuming the steady-state hypothesis ($L_i = G_i$). For each node, the ingoing fluxes are then distributed across resource nodes according to the consumer's preferences, described in a separate matrix (Gauzens et al., 2019).

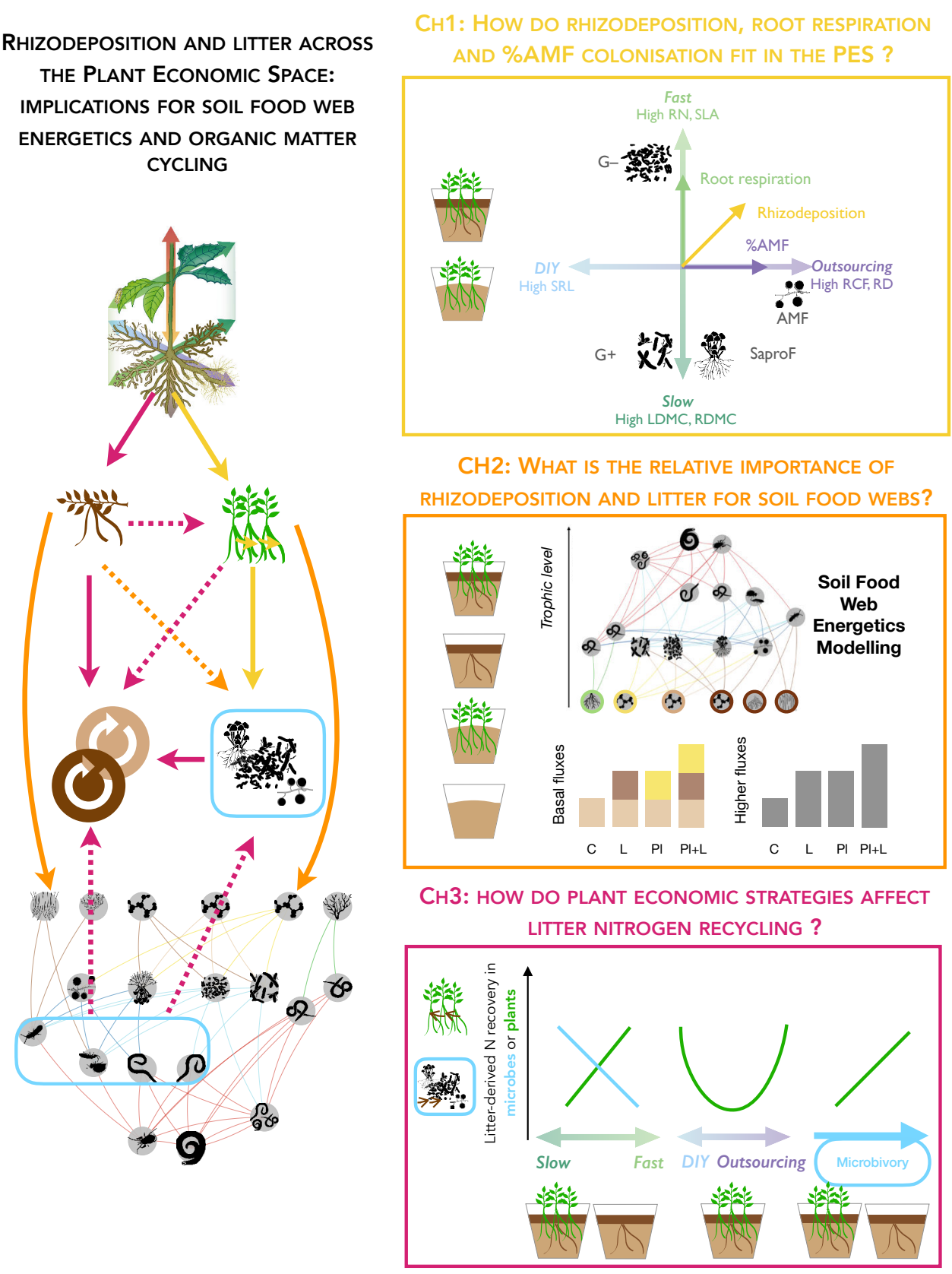
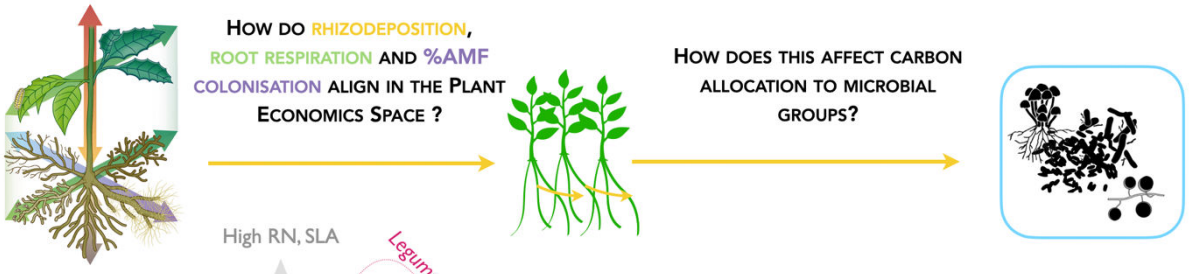


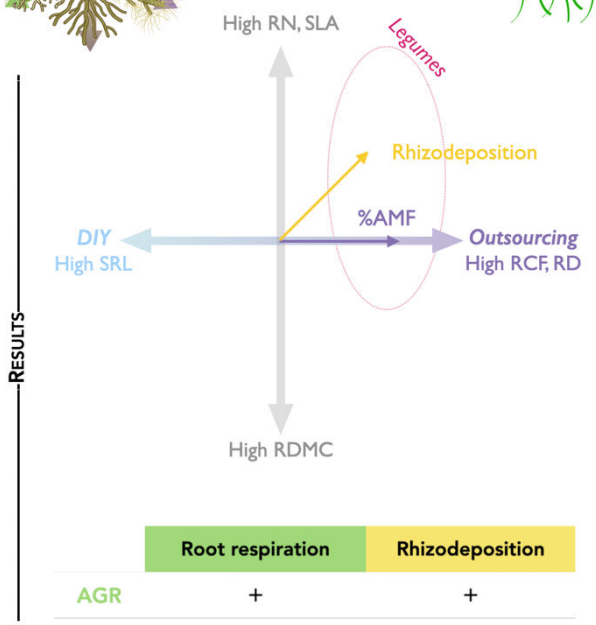
Figure 21 Overview of the three chapters and their respective hypotheses

The central figure shows how these questions are integrated in the interactions between the plant economic strategies and how they affect plant inputs, their impact on microbial communities and SOM cycling (including litter decomposition) and soil food webs.

Chapter 1

Do roots physiological traits and carbon allocation to microorganisms fit in the plant economics space framework?





PLFAs	Biomass	Enrichment
SpRR		+ (AMF only)
Rhizo	+ (Zygomycota only)	+ (except Zygomycota)
%AMF	+ (AMF only)	
⟷	AMF, G+	AMF, G–

	Root respiration	Rhizodeposition
AGR	+	+

Abstract

Context. The plant economics *spectrum* describes resource acquisition strategies trade off opposing fast growing acquisitive species to slow growing conservative ones. Its recent extension, the plant economics *space*, acknowledges the multidimensionality of root traits by including an independent trade-off describing plant belowground exploration strategy, spanning from "do-it-yourself" species who invest in morphologically efficient root systems to "outsourcing" species who rely on mycorrhizal fungi for this essential function. If aboveground physiological traits are well integrated in this framework (acquisitive species tend to have higher metabolic rates, higher respiration and higher photosynthesis), evidence on how belowground physiological traits like root respiration, degree of arbuscular mycorrhizal fungi (AMF) colonisation and rhizodeposition fit in this framework is scarce.

Methods and objectives. Here, we investigate the position of these three physiological traits in the plant economics space across 15 grassland species in a common garden experiment including a litter addition treatment. We further dive into how plant strategy, especially rhizodeposition, characterised by ^{13}C pulse labelling, affect the microbial community by measuring PLFAs relative biomass and ^{13}C enrichment.

Results. We found that physiological traits fitted coherently in the PES, with higher root respiration in fast growing species, higher degree of AMF colonisation in outsourcing species, and higher rhizodeposition in legumes, who are both acquisitive and outsourcing species. Traits that usually characterise the fast/slow gradient (specific leaf area, leaf and root dry matter content (RDMC), leaf and root nitrogen content (LNC)) were not correlated as expected with absolute growth rate. All microbial groups were dependant on recent photosynthates, and to the exception of saprotrophic fungi, microbial enrichment was positively associated to rhizodeposition. AMF relative biomass but not enrichment was associated with higher degree of colonisation. Litter addition barely impacted the microbial community, but affected differentially root traits, promoting higher absolute growth rate, degree of colonisation, and RDMC, and lower specific root length and RNC.

Discussion. Our results support the plant economics space and demonstrate that plant influence on microbial groups is mediated by rhizodeposition, though biomass and enrichment give complementary information. With our litter addition treatment, we also highlight how plant intraspecific variability may blur the strategy/trait linkage.

1. Introduction

Plants have developed many different strategies to survive and grow in a wide range of environmental conditions and resource availability (Grime, 1977). Various theoretical frameworks describing these plant strategies relative to the acquisition, processing, and conservation of resources have been developed, mostly based on sets of functional traits (Díaz et al., 2016; Reich, 2014). In the Plant Economics Space (PES) framework (Reich, 2014; Weigelt et al., 2021), carbon is a currency invested to gain other resources like water, light and nutrients.

The "fast-slow gradient" represents the trade-off between growth and survival: investment in longer-lasting organs with low metabolic rates (slow-growing/conservative species) or investment in more disposable organs with high metabolic rates (fast-growing/acquisitive species). Primarily developed to describe the variation of leaf traits (Wright et al., 2004) in the "leaf economics spectrum" (LES), this framework has then been extended to other organs (Reich, 2014), as strategies are supposedly coherent across organs (roots, leaves and stems) and resources (water, carbon and nutrients). Conservative species are characterised by roots and leaves with high tissue density (RTD, LTD) and high dry matter content (RDMC, LDMC). Contrariwise, high relative growth rate (RGR), high specific leaf area (SLA) and with high nitrogen concentration in roots and leaves (RNC, LNC) are typical of acquisitive species (Craine et al., 2005; Reich, 2014; Weigelt et al., 2021).

However, belowground traits do not always align with the LES (Kramer-Walter et al., 2016; M. Zhou et al., 2018): for example, specific root length (SRL), which was considered analogous to SLA is sometime aligned and sometime orthogonal to the fast/slow gradient. The PES framework has newly resolved this issue by including an additional syndrome of root traits called the "collaboration gradient" (Bergmann et al., 2020; Weigelt et al., 2021). It represents the trade-off between (i) "externalisation" of soil exploration and belowground resource acquisition to arbuscular mycorrhizal fungi (AMF), a strategy associated with high root diameter (RD) and high cortex fraction (CF) and (ii) investment in a plant's own exploration system – the "do it yourself" strategy (DIY) – associated with a higher SRL. This collaboration gradient has also been termed the "morphological efficiency" of belowground acquisition (Sun et al., 2021). We will hereafter name it the "exploration gradient", to encompass the morphological trade-off while avoiding confusion with mutualistic interactions with non-mycorrhizal microorganisms in the rhizosphere.

Relationships between aboveground physiological and morphological traits are well documented (Marino et al., 2010; Onoda et al., 2017; Reich et al., 2008; Wright et al., 2004). Conversely, belowground physiological traits such as root respiration, rhizodeposition and arbuscular mycorrhization have only recently been investigated in light of the plant economics space (Guyonnet, Guillemet, et al., 2018; Han & Zhu, 2021; Williams et al., 2022), and there is still much to unravel, as studies including more than one belowground physiological trait are scarce (Henneron, Cros, et al., 2020; Sun et al., 2021). The relationship of mycorrhizal colonisation, root respiration and rhizodeposition with other traits is of major significance

for the PES framework, as two of them (AMF colonisation and rhizodeposition) are directly involved in resource acquisition, and all these physiological processes are huge carbon sinks for plant carbon.

Plants allocate 10-20% of their photosynthates to arbuscular mycorrhizal fungi (AMF) and up to 50% to ectomycorrhizal fungi (van der Heijden et al., 2015), and mycorrhization is a strategy explicitly representing one pole of the exploration gradient. However, most studies on belowground economics space only use the opposition between RD and SRL as a proxy for mycorrhization potential and take into account mycorrhizal type (Carmona et al., 2021; Weigelt et al., 2021), while relatively few studies actually report measurements of mycorrhizal colonisation and test its relationship with the exploration gradient (Bergmann et al., 2020; Z. Ma et al., 2018; Matthus et al., 2025). Indeed, the relationship between morphological traits and AMF colonisation is supposedly very strong, because tightly linked to evolutionary history (Z. Ma et al., 2018). Yet, environmental conditions affect mycorrhizal colonisation: for example, in case of high nutrient availability, plants tend to have lesser AMF colonisation (Corkidi et al., 2002; Šmilauer et al., 2021). Furthermore, though AMF do not possess the enzymes necessary for decomposing organic matter like ectomycorrhizal fungi do, they can still rely substantially on litter to meet their own nitrogen need (Hodge & Fitter, 2010), probably absorbing N mineralised by hyphosphere bacteria. Access to a patch of organic matter has also been shown to promote hyphae growth and foster colonisation of another plant (Hodge et al., 2001; Hodge & Fitter, 2010). Thus, it remains unclear whether litter addition would (a) lead to a decline in mycorrhizal colonisation due to the addition of nutrients to the soil, or (b) the opposite, AMF being promoted as efficient support for the exploration of decomposing litter patches.

Grassland species' roots respire around 6% of gross primary production (GPP), which represent 20% of carbon allocated belowground (Pausch & Kuzyakov, 2018). Respiration is a metabolic process that is essential for both growth and maintenance, through ATP production and redox balancing, and has been associated with plant resource acquisition (Han & Zhu, 2021). Indeed, respiration is a direct measure of metabolic activity (Brown et al., 2004), and the "fast-slow gradient" also corresponds to a fast-slow metabolic activity (Reich et al., 2008; Sun et al., 2021). In a meta-analysis compiling 245 woody and non-woody plant species, Han & Zhu (2021) found root respiration to be correlated positively with RNC and negatively with root tissue density (RTD), while they found no or weak relationships with SRL and RD. Therefore, root respiration can be expected to be associated with the fast-slow gradient, reflecting both construction costs/life span trade-offs (Hou et al., 2024) and metabolic efficiency. According to the PES described by Weigelt et al. (2021), we would thus expect AMF colonisation and root respiration to be independent. However, it might not be so simple, as there are also indications of AMF colonisation inhibiting root respiration (Sun et al., 2021; Wen et al., 2021). This contrasted evidence pleads for more investigation of belowground physiological traits linkages in the PES framework, also including rhizodeposition, which is particularly challenging to study (Oburger & Jones, 2018).

Grassland species allocates around 10% of GPP to rhizodeposition, *i.e.* the release of organic compounds by living roots (Pausch and Kuzyakov, 2018). Rhizodeposition and rhizosphere processes mediated by microbes are essential for soil organic matter (SOM) cycling. Root exudates are now considered as a major source of new soil organic matter (Sokol, Kuebbing, et al., 2019; Villarino et al., 2021), but they can also destabilise old mineral-organic association and promote microbial activity (Dijkstra et al., 2021). This can lead to increased SOM mineralisation (Henneron, Cros, et al., 2020; Keiluweit et al., 2015), resulting in higher nitrogen availability (Craine et al., 2007; Henneron, Kardol, et al., 2020; Kuzyakov & Xu, 2013). This motivates the hypothesis that high rhizodeposition is an attribute of acquisitive species (Wen et al., 2021). While there is strong evidence for the association of rhizodeposition with the fast-slow gradient (Henneron, Cros, et al., 2020; Sun et al., 2021), its relationship with the exploration gradient is unclear. While Guyonnet, Cantarel, et al. (2018) found a positive correlation between rhizodeposition and SRL, Williams et al. (2021) found a positive correlation between root exudation and root diameter, while other did not find any relationship between rhizodeposition and the exploration gradient (Henneron, Cros, et al., 2020; Sun et al., 2021). Zhou et al. (2020) found that AMF colonisation enhanced rhizodeposition up to 33% in tomatoes. Indeed, most of the rhizosphere processes described above can also occur in the hyphosphere and transit through AMF (Huang et al., 2021; Shahzad et al., 2015), maybe with a higher efficiency: Kaiser et al. (2015) found that ^{13}C signal from recent photosynthates increased faster in microbial PLFAs from the hyphosphere than in those from the rhizosphere.

Soil microbes mediate most of processes relevant for ecosystem functioning in soils. Research on microbial functional groups is currently undergoing significant development but the intrinsic differences between fungi and bacteria have been documented for decades. Fungi have higher biomass, C:N ratio and carbon use efficiency but lower turnover time and respiration rate (X. Wang et al., 2019; Waring et al., 2013). Saprotrophic fungi also have the enzymatic kit for degrading recalcitrant compounds like lignin and cellulose, and are therefore the primary decomposer, while bacteria feed litter soluble leachates or products from fungal extracellular decomposition, and thrive in the rhizosphere where roots supply exudates composed of easily available carbon (de Boer et al., 2005; Wardle, 2004). However, a recent meta-analysis established that saprotrophic fungi also incorporate recent photosynthates exudated by plant roots (Huang et al., 2020), and demonstrated that they are able to compete for various carbon sources within and outside of the rhizosphere (Elfstrand et al., 2008; Huang et al., 2020), similarly to Gram- bacteria. On the other hand, Gram+ bacteria have an affinity for recalcitrant substrate (Fanin et al., 2013; Huang et al., 2020), and are more related to litter (Elfstrand et al., 2008) and SOM carbon (Kramer & Gleixner, 2008). Ecosystem with a lower ratio of fungal over bacteria (*f:b* ratio) tend to have higher productivity (De Ruiter et al., 2005). Acquisitive species have been shown to promote bacteria over fungi, especially Gram– bacteria (de Vries et al., 2012; X. Wan et al., 2021), but these studies focused on PLFAs relative biomass, not allocation of recent photosynthates to microbial groups, which may give more insight on the mechanisms involved in this relationship.

Here, we aimed at advancing our knowledge of the relationships of physiological root traits (root respiration, root mycorrhization and, rhizodeposition) with the leaf and root economics space, and to question how plant strategy affects allocation of carbon from rhizodeposition to soil microbial groups, and explored how the presence of litter could affect these patterns. To do so, we grew 15 grassland species with contrasted economic strategies with and without litter addition in a mesocosm experiment. We followed the fate of recent photosynthates across plant and microbial groups with ^{13}C pulse labelling.

First, we hypothesised that AMF colonisation primarily aligns with the cooperative strategy and root respiration primarily aligns with the acquisitive strategy, while rhizodeposition would show positive relations with both (Figure 1). Second, we anticipated microbial community to shift under the influence of plant strategy, both in terms of community structure and assimilation of recent photosynthates. Specifically, we expected higher relative concentration and higher allocation of plant photosynthates in AMF PLFA when root AMF colonisation is higher, as well as in Gram– bacteria markers under more acquisitive species. Last, we expected our conclusion to be stable with and without litter addition, though the presence of litter may affect AMF colonisation and change the balance between microbial groups, favouring fungi and G+ bacteria.

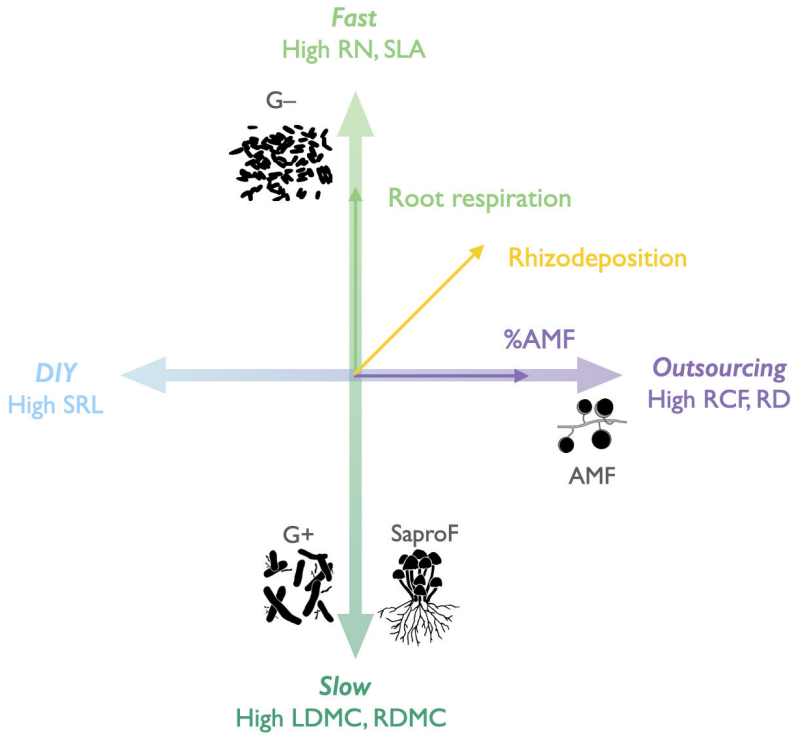


FIGURE 1 Schematic representation of our hypotheses

2. Material and Methods

2.1. Experimental design

Our experiment includes 15 grassland species from three functional groups (legumes, grasses, and non-leguminous forbs), grown in 6 L (20 cm-deep) monospecific pots with or without litter addition for 3 months in an experimental garden at 49°27'27.9"N 1°04'06.0"E, Mont Saint Aignan, France. Species were selected for their contrasting strategies on two gradients, based on *a priori* traits. For each species, we aimed to have plant-only (P), and plant+litter (Pl+L) treatment, replicated three times, but due to insufficient litter production for *Campanula rotundifolia* and *Nardus stricta*, both species solely have the plant-only treatment. Pots were handled in three blocks, each block containing one replicate of the 15 species plants-only treatment, 13 pots with plant and litter treatment, as well as 2 pots with only soil – namely a total of 86 pots. Seeds came from Caen and Rennes botanical gardens, Jelitto or Semences du Puy.

The soil used was collected from the 20 first centimetres of a permanent urban mesophilic grassland (49°28'28.3"N 1°04'17.6"E Mont Saint-Aignan, France). Soil was sieved at 5 mm and a visual sorting of macrofauna was performed to remove earthworms, eggs and click beetle larvae. Pots were filled at a soil volumetric mass density of 0.8 $kg.L^{-1}$.

Litters were produced in hydroponics conditions in a WeissTechnik SGC fitotron, with a 16 hour-daylight period, in a nutritive solution (Hoagland, 1920), with 0.2 g/L of 10%-enriched $K^{15}NO_3$ in order to trace nitrogen fluxes from litter decomposition for another study. The growth period lasted between 2 and 4 months, depending on species productivity, and was followed by a 1–3-week(s) senescence period induced by progressively cutting water supply. Litters were then sorted between shoot and roots, washed and dry up at 40°C. For the Pl+L treatment, 0.7 g of root litter was incorporated in the first 7 cm of the pots and 1.5 g of shoot litter was deposed on the surface and roughly mix with the first centimetre to prevent scattering due to wind. These values are calculated from average grassland productivity (Scurlock et al., 2002) converted to litter production according to Cebrian and Lartigue (2004) corrected by the density of our pots.

Before seedling transplantation pots were saturated with water for both measure of field capacity and evacuation of a potential N-flush caused by sieving. Seedling have been germinated until 2 leaves stage, preserved at 4°C for synchronisation between all species, and 7 individuals were transplanted in each pot in the experimental garden. Dead seedlings were replaced until the 5th week of the experiment. Pots were kept over 60% of field capacity for the duration of the experiment.

2.2. ^{13}C pulse labelling

From September 12th, we handled one block per week (each block containing one replicate of each treatment), with the following steps. All 28 pots with living plants were labelled during 6 hours for two consecutive days, with 10% $^{13}CO_2$ in a 2 m^3 hermetic chamber linked to an infrared CO_2 analyser (LI-830,

LI-COR Biosciences) during two consecutive days, with 6 hours of labelling for each day. The CO_2 concentration inside the chamber was doubled (from 450 ppm to 900 ppm) by adding CO_2 produced from the reaction of H_2SO_4 over of a 20% enriched $Na_2{}^{13}CO_3$ solution according to Pang et al. (2021). Chamber CO_2 concentration was then maintained between 750 ppm and 900 ppm throughout the labelling by regular addition of 10% enriched $^{13}CO_2$ obtained by the same reaction. Inside the chamber, three fans allowed the even distribution of the gaz. Between the two days of labelling, the chamber was opened to avoid CO_2 accumulation due to overnight respiration. Light was provided by 125 W compact fluorescent lamps, which supplied between 100 and 250 µmol/m^2/s of photosynthetically active radiations (measurements at different heights in the chamber, with a Li6400, LI-COR Biosciences), which is far under natural light value but usual in growth chamber experiment (Belluau and Shipley, 2018; Shipley, 2006).

2.3. Plant economic traits

2.3.1 Harvest and trait measurements

On the third day after the beginning of the labelling process, 10 leaves were collected from the 7 individuals to measure leaf traits (fresh weight, scan, C and N concentration) before the rest of the harvest. All leaf traits were measured on the 10 leaves per pots sampled on harvest day, except for above-ground isotopic signal that was measured on a mix of all above-ground parts and leaf respiration and photosynthesis (described above).

We sampled and washed roots mixed from three 16 cm-deep (whole pot) core samples collected at the barycentre of three plants to measure fine root traits (root respiration, fresh weight, scan). Fine root respiration was measured within 10 hours after sampling (on sample stored at 4°C in humid plastic bags) using a Li830 CO_2 analyser coupled to a chamber kept in a 23°C bain-marie. Samples were acclimated in the bain-marie for 5 minutes prior to measurement according to Lak et al. (2020). All scans were performed with an Epson Expression LA2400 Scanner and analysed with WinRhizo Pro 2020 and WinFolia Pro 2020, with standard thresholds, within 48h after harvest (conserved at 4°C). We used measures of leaf area (cm2), root length (cm), and root mean diameter (mm). Fresh weights were measured right after scanning. Specific root length (SRL) was calculated as total length divided by root dry mass, specific leaf area (SLA) was calculated as leaf area divided by leaf dry mass, and dry matter content was calculated as dry mass divided be fresh mass for both roots and leaves. Contrary to the studies proposing the framework (Bergmann et al., 2020; Weigelt et al., 2021), we used RDMC instead of root tissue density (RTD) in our analyses, because RTD calculated with WinRhizo may be overestimated when considering roots of variable class diameter (Rose, 2017), and RDMC is a very good proxy of true RTD (R^2 = 0.9, Birouste et al., 2014).

One individual's root system was sampled immediately, washed, dried and powdered to measure ^{13}C signature, estimating below allocation of recent photosynthates. After harvest, pots were store at 4°C for

2-4 weeks before the rest of the root system could be sorted, washed up and dried. All vegetation samples were dried at 35°C for at least 48h.

AMF colonisation was determined at x200 magnification on 10 points of 10 stained fragments (1 cm) of these dried fine roots and AMF colonisation, according to McGonigle et al. (1990).

N and C content of leaves and roots were measured on an elemental analyser (Flash, 2000; Thermo Fisher Scientific, Cambridge UK). Stable isotope concentration of above- and below-ground parts were measured with a Delta V Advantage Thermo Electron (Bremen, Germany) isotope ratio mass spectrometer (IRMS) at the Centre for Stable Isotope Research and Analysis (University of Göttingen).

2.3.2 Rhizodeposition

Quantity of rhizodeposits produced between the beginning of the labelling and the harvest was estimated from the quantity of label recovered from the fumigated soil extracts (label assimilated by rhizosphere microbes and in dissolved organic matter) and the quantity of label recovered in CO_2 after a 24h soil incubation (label respired by rhizosphere microbes), which allowed us to estimate gross rhizodeposition.

30 g of dry-soil equivalent were incubated at 23°C in airtight pots filled up with CO_2-free atmosphere, and soil moisture was standardized at 60% ± 10% of water holding capacity. To estimate soil respiration, 5 mL of incubation pot atmosphere was injected in a closed circuit filled with N_2 linked to an infrared CO_2 analyser (LI-830, LI-COR Biosciences). Original concentration was determined with a calibration curve made from 5 mL injection of 5 known concentrations (0, 500, 1000, 5 000, 10 000 ppm) just before the measurements ($R^2 > 0.99$). To estimate the ^{13}C isotopic signature of respired CO_2, 5 mL of atmosphere from the incubation pot was and analysed on an isotope laser spectrometer (CRDS Analyzer, Picarro) after storage (4°C, 18 months). Enrichment was calculated as Atom Percentage Excess (APE), and expressed in ppm.

$$APE = (atom\%)_{enriched} - (atom\%)_{baseline}$$

For soil and microbial parameters, the baseline was calculated as the mean atom% of unlabelled pots (the 6 control pots and 39 pots with litter addition only, used for another experiment), while for plants, it was calculated from the plants grown in hydroponics for litter production, with a specific baseline for each species.

Rhizodeposition per gram soil (µmolC g soil^{-1}) was calculated as:

$$RhSoil = (APE_F \times n_{C_F} + \mathrm{APE}_{Incub} \times RespRate_{C_{Incub}} \times 48) \times \frac{1}{LI}$$

where APE_F and APE_{Incub} are the enrichment of the fumigated extract and the CO_2 produced during the soil incubation (ppm), n_{C_F} refers to the amount of carbon in the fumigated extract (molC g soil^{-1}), $RespRate_{C_{Incub}}$ is the respiration rate assessed during the incubation (molC g soil^{-1} hour^{-1}), 48 hours is the time between the beginning of the labelling and the beginning of the harvest and LI is the labelling intensity (%), which is block dependant, with the aim of 10% being more or less attained, depending on the amount of replenishment of the labelling chamber.

TABLE 1 – Overview of studied traits

**i.e. strategy associated with high attribute in this trait*

Type	***Abbr.***	***Trait***	***Unit***	***Associated strategy****
Chemical	LNC	Leaf Nitrogen Content	%	Acquisitive
Chemical	RNC	Root Nitrogen Content	%	Acquisitive
Morphological	SLA	Specific Leaf Area	cm^2 g root^{-1}	Acquisitive
Morphological	LDMC	Leaf Dry Matter Content	%	Conservative
Morphological	RDMC	Root Dry Matter Content	%	Conservative
Morphological	RMD	Root Mean Diameter	mm	Outsourcing
Morphological	RCF	Root Cortex Fraction	-	Outsourcing
Morphological	SRL	Specific Root Length	cm g root^{-1}	DIY
				Hypothesis
Physiological	SRR	Specific Root Respiration	µmolC s^{-1} g root^{-1}	Acquisitive
Physiological	SRh	Specific Rhizodeposition	µmolC g root^{-1}	Acquisitive/ Outsourcing
Physiological	RhSoil	Rhizodeposition (per gram soil)	µmolC g soil^{-1}	Acquisitive/ Outsourcing
Physiological	%AMF	Percentage of root colonized by AMF	%	Outsourcing
Allocation	PropRh	Proportion of label recovered in soil respiration and microbial biomasss	%	Acquisitive/ Outsourcing

2.3.3 Soil microbial communities

Soil from the three 7 cm-deep core samples, each collected at the barycentre of three plants was sieved at 2 mm before further analysis. Soil microbial biomass was determined by the fumigation-extraction method according to ISO 14240 (1997), modified using an extractant concentration of 0.2 mol/L K_2SO_4 solution to facilitate following isotopic measurement on lyophilised extract (Makarov et al., 2015).

Other subsamples were frozen, lyophilised and the three replicates of the same species for the same treatment were pooled for phospholipids fatty acids (PLFA) extraction and derivatisation, following the protocol of Frostegård et al. (1993) to investigate the structure of the microbial community. Concentrations of resulting phospholipid methyl esters were analysed with a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA) while their ^{13}C isotopic signature was assessed at the Centre for Stable Isotope Research and Analysis (University of Göttingen) on a Thermo Finnigan Trace Gas Chromatograph coupled via a GP interface to a Delta V mass spectrometer (Thermo, Bremen, Germany). Assignation to microbial functional groups followed Joergensen (2022)'s classification. 16:1w7, cy17:0, cy19:0, 18:1w7 and cy19:0 were considered as Gram– markers; i15:0, a:15:0, i16:0 and i17:0 were considered as Firmicutes (Gram+) markers, 18:2w6,9 and 18:1w9 were considered fungal markers (respectively from Ascomycota/Basidiomycota and Zygomycota phyla) while 16:1w5 was used as an AMF marker. We had planned to group Ascomycota/Basidiomycota in a unique "saprotrophic fungi" group, but 18:2w6,9 was not detected in isotopic analysis, so we only present Zygomycota's enrichment.

Microbial group enrichment was calculated as the averaged enrichment (APE_{PLFA_i}) of this group's PLFAs, weighted be each PLFA concentration ($[PLFA_i]$) and number of C atom.

$$APE_{group} = \frac{\sum_{PLFA_{group}} APE_{PLFA_i} \times [PLFA]_i \times n_{C\,PLFA_i}}{\sum_{PLFA_{group}} [PLFA]_i \times n_{C\,PLFA_i}}$$

2.4. Statistical analysis

Statistical analyses were conducted with the R version 4.4.1. For each trait, we determined the coefficient of variation (CV = standard deviation/mean) at specific, functional group and complete dataset level. We also assessed intraclass correlation using a model with species and functional group as random effects. Because intraspecific variability was comparable to some interspecific variability for certain traits, we chose not to pool replicate from the same species, as our focus is on relationships between traits (Figure S1, Figure S2). To assess the effect of litter addition on the traits we measured, we used a log-response ratio, calculated as $\ln RR = \log(Trait_{Pl+L}/Trait_{Pl})$, which we tested with a U-Mann Whitney test against a null hypothesis corresponding to $\ln RR = 0$ (no litter addition effect). For each trait which showed a litter addition effect, we also compared the mean of $|\ Trait_{Pl+L}/Trait_{Pl} - 1\ |$ across replicates with the specific coefficients of variation to coarsely evaluate whether the litter addition effect was similar to intraspecific variability. If this measure was higher than specific CV, we considered that it reflected high trait plasticity

in response to litter addition, while a value lower than specific CV was interpretated as high trait conservation. We acknowledge that this comparison is unorthodox, but we argue that it provides interesting insights.

To study the variation in syndromes of traits rather than individual traits, all eight morpho-chemical traits were included in a principal component analysis (PCA, Figure 2). PCA was computed using *FactoMineR::PCA*, on a dataset completed for missing values (13% for root cortex fraction, less than 2% for other morpho-chemical traits) with *MissMDA::imputePCA*. The first two PCA axes (representing together more than 50% of the inertia) were included in further models. The only trait that was not well represent by either axis was LDMC, who loaded on dimension 3 (Figure S3). Physiological traits were included as supplementary variables.

We investigated the relationship between physiological traits and the PES using linear mixed models (Equation 1) and relationship of physiological traits with microbial groups biomass and APE (atom percentage enrichment) using linear models (Equation 2). Indeed, as the PLFAs were measured on pooled samples, there is no need for random effect "Block".

$$PhT = \beta_0 + \beta_L L + \beta_{nod} nod + \beta_{AGR} AGR + \beta_{PCA1} PCA1 + \beta_{PCA2} PCA2 + b_B B + \epsilon \quad (1)$$

$$M = \beta_0 + \beta_L L + \beta_{nod} nod + \beta_{AGR} AGR + \beta_{PCA1} PCA1 + \beta_{PCA2} PCA2 + \sum_{PhT} \beta_{PhT} PhT + \epsilon \quad (2)$$

where *PhT* is one of the physiological traits of interest among RhSoil, SpRh, SpRR, and %AMF, *L* litter addition, *AGR* is the absolute growth rate, *PCA1* and *PCA2* are the coordinates on the PCA axis, *nod* is the capacity of a species to form nodules and *M* is a microbial parameter among relative biomass or APE. β are the fixed-effects coefficients, b_B are the coefficients for the block random-effects, and ϵ are the residuals errors.

Models were computed using the *lme4::lmer* function on data sets previously z-scored scaled, allowing to compute standardised regression coefficients that can easily be compared (β). To improve residuals normality, variables (except PCA axes) were transformed using ln(x) or logit(x) for percentages before scaling. *Rumex acetosa* was excluded from the data when assessing relationship between %AMF colonisation and economic strategies, as it is a non-mycorrhizal species.

We performed model selection with *MuMIn::dredge* based on AICc, starting from the saturated model presented in Equations 1 and 2 fitted with maximum likelihood (REML = F). When more than one model had a ΔAICc < 2 to the smallest AICc, we performed model averaging on models with ΔAICc < 2 with *MuMIn::model.avg*. We report coefficients averaged on the full subset (coefficient considered equal to 0 when not present), as it is the most conservative estimation, and the R^2 of the best model (adjusted R^2 for linear models, and marginal (R^2m, including only the fixed effect) and conditional (R^2c, including both fixed and random effect) coefficient for linear mixed models, calculated with the *MuMin* package).

3. Results

3.1. Syndromes of traits between plant strategies

3.1.1 Overview of trait syndromes

Using a PCA, we identified trait syndromes reflecting the exploration trade-off (Figure 2A). SRL and RMD contributed most (> 20% each, Figure S1) to the first PCA axis (PCA1, explaining 37.1% of total variation), with opposite loading ($PCA1_{SRL}$ = -0.85, $PCA1_{RMD}$ = 0.91), reflecting the exploration trade-off, with outsourcing strategy associated with positive values, and DIY with negative values, respectively. RCF and RNC also contributed to the first axis (> 15% each), with positive scores ($PCA1_{RCF}$ = 0.73, $PCA1_{RNC}$ = 0.67). LDMC scored on PCA1 ($PCA1_{LMDC}$ = -0.47), despite a low contribution (< 10%). Rhizodeposition per gram soil and %AMF colonisation, plotted as supplementary variables, loaded on PCA1 ($PCA1_{\%AMF}$ = 0.28, $PCA1_{RhSoil}$ = 0.36), with a positive correlation with this PCA axis for rhizodeposition per gram soil (R = 0.43, p < 0.001, Figure S4). Notably, some *Holcus lanatus* and *Anthoxantum odoratum* pots also displayed high rhizodeposition per gram soil and high SRL but not enough

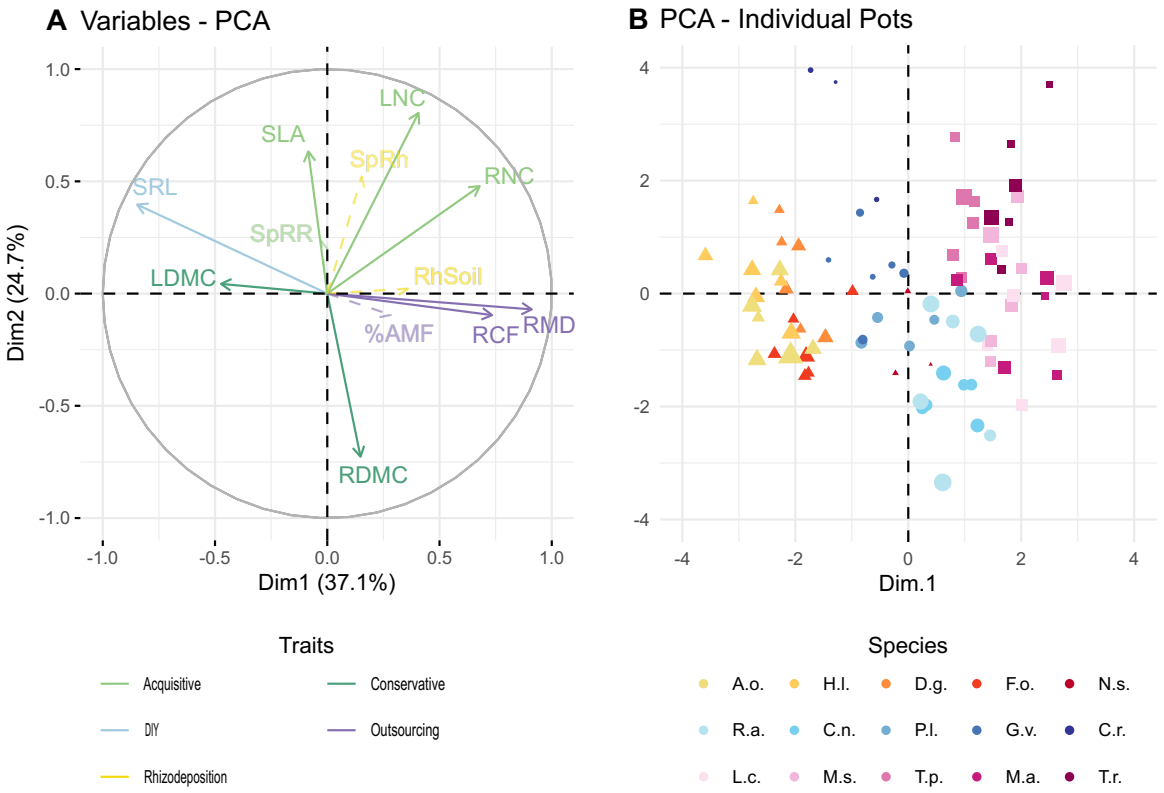


FIGURE 2 Principal component analysis on above and belowground morpho-chemical traits, growth rate and physiological traits

Variable colours (A, C) indicate the strategy associated with high values in this variable: light green/acquisitive, dark green/conservative, light blue/DIY, purple/cooperation. Transparent dotted variables are supplementary variables. Points' colour and shape (B, D) indicate functional groups (orange triangle: grasses, pink square: legumes, blue disk: forbs), while size reflect growth rate (bigger points have higher growth rate).

for rhizodeposition to be correlated with PCA1[2] (Figure S4). This axis also separated plant functional with grasses having negative values, legumes positive values and forbs loading close to 0 (Figure 2B).

The second PCA axis (PCA2, explaining 24.7% of total variation) was formed primarily by the contribution (> 20% each) of LNC ($PCA2_{LNC} = 0.80$), RDMC ($PCA2_{RMDC} = -0.72$), and SLA ($PCA2_{SLA} = 0.63$), SRL and RNC also loaded secondarily on this axis ($PCA2_{SRL} = 0.40$, $PCA2_{RNC} = 0.48$). Specific rhizodeposition and specific root respiration, plotted as supplementary variables, loaded on PCA2 ($PCA2_{SpRh} = 0.52$, $PCA2_{SpRR} = 0.24$), with a positive correlation to this PCA axis for specific rhizodeposition ($R = 0.47$, $p < 0.001$, Figure S4). Species with high AGR were found both on positive and negative values of the first and second axes (Figure 2B), thus impairing the interpretation of this second dimension as the fast/slow trade-off, and justifying the inclusion of AGR as a separate variable in the models (see § 4.1).

Both rhizodeposition measurements were correlated with each other ($R = 0.31$, $p < 0.01$, Figure S4), but showed opposite relationships to AGR, with specific rhizodeposition being negatively correlated with AGR ($R = -0.36$, $p < 0.001$) while rhizodeposition per gram soil was positively related ($R = 0.43$, $p < 0.001$).

3.1.2 Modelling physiological traits with plant economic strategy

Using linear mixed models, we tested if plant strategy (PCA scores, AGR and ability to form nodules) was a good predictor of physiological traits, in order to assess whether physiological traits were aligned with the PES.

%AMF colonisation was higher for "outsourcing" strategy, i.e., individuals scoring higher on PCA1 ($\beta_{PCA1} = 0.47 \pm 0.36$, $p < 0.05$) and in presence of litter ($\beta_{L} = 0.46 \pm 0.43$, $p < 0.05$). Specific root respiration was positively associated with both AGR ($\beta_{AGR} = 0.53 \pm 0.23$, $p < 0.01$) and higher score on PCA2 ($\beta_{AGR} = 0.45 \pm 0.26$, $p < 0.001$). Rhizodeposition per gram soil was also associated with lower scores on PCA2 ($\beta_{PCA2} = -0.31 \pm 0.23$, $p < 0.01$), while specific rhizodeposition was negatively related to AGR ($\beta_{AGR} = -0.54 \pm 0.18$, $p < 0.001$). The ability to form nodules was positively associated with both rhizodeposition per gram soil and specific rhizodeposition ($\beta_{nod} > 0.8$, $p < 0.001$).

The fixed effects in the best models for each trait explained a weak to moderate proportion of the variation. R^2m was successively 0.23 for %AMF colonisation, 0.27 for both specific rhizodeposition and rhizodeposition per gram soil and lastly 0.35 for specific root respiration. The models selected for model averaging represented over 50% of AICc weight (Figure 3, Table S3).

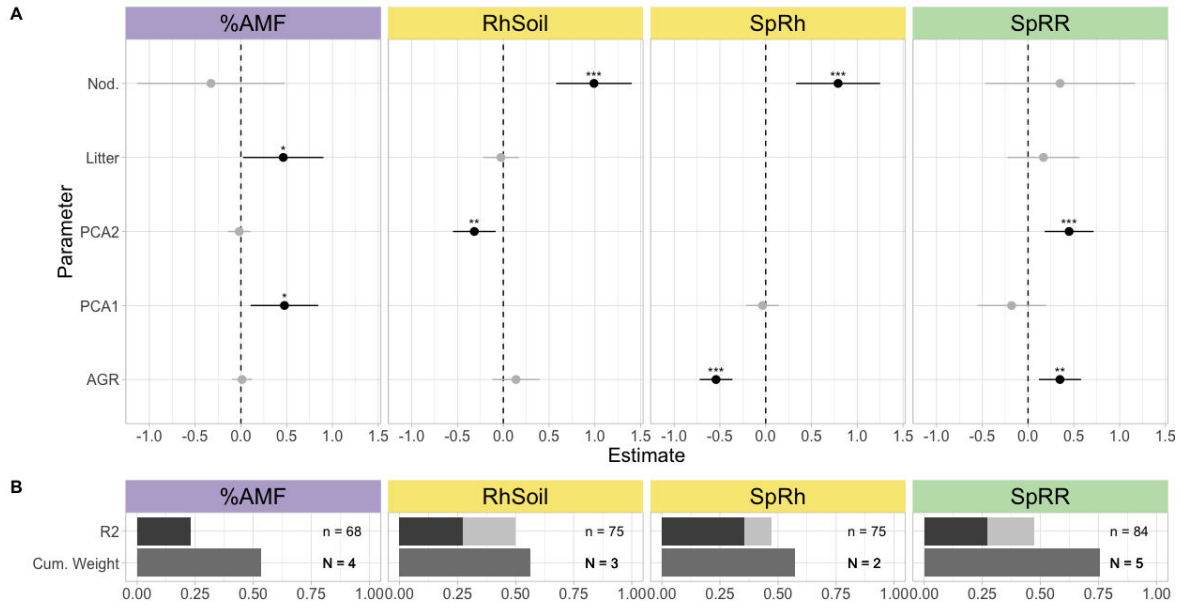


FIGURE 3 Model summary of physiological traits predicted by plant strategy

$$PhT = \beta_0 + \beta_L L + \beta_{AGR} AGR + \beta_{PCA1} PCA1 + \beta_{PCA2} PCA2 + \beta_{nod} nod + b_B B + \epsilon$$

*Summary of standardised coefficient for physiological traits, from model averaging. Points indicate coefficient estimate, lines reflect 95% confident interval (CI), both are in black if the CI does not intersect with 0. *: p< 0.05, **: p<0.01, ***: p <0.001. The R^2c (dark grey) and R^2m (light grey) of the best model (ΔAIC =0) and the cumulative weights of averaged models (grey) are reported in panel B. Note that the random component was not significant for %AMF colonisation.*

3.1.3 Modulation of trait syndromes by litter addition

According to log-response ratio (Figure 4), litter addition affected positively %AMF colonisation, AGR, RCF and RDMC and negatively RNC and SRL. The largest differences are the 60% higher %AMF colonisation and 20% higher AGR in presence of litter, other being around ± 10%. Those differences are not reflected in the first two PCA axes. Interestingly, the absolute response ratio had ranges similar to trait coefficient of variations (15-30%) for AGR, RCF and RDMC, but for %AMF, the response ratio was more than twice higher than the CV (190% vs 90%), while it was around three times lower than the CV for RNC and SRL (14% vs 48% and 25% vs 66%, respectively, figure S2B).

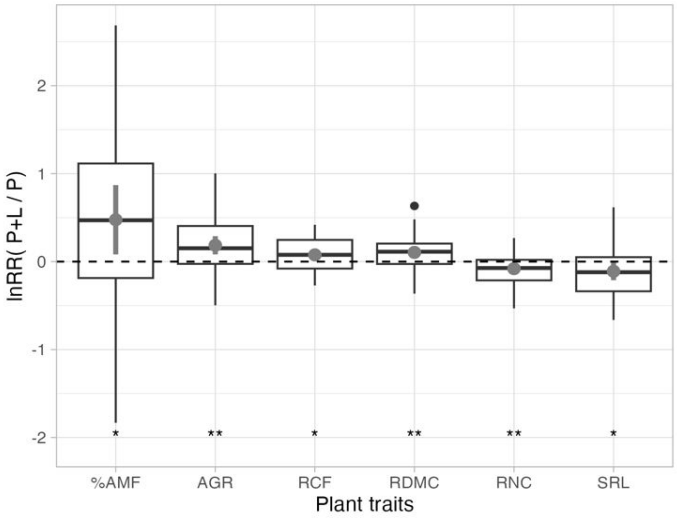


FIGURE 4 Log Response Ratio of various traits to litter addition

Boxplots show the median, as well as 1st and 3 quartiles (hinges), whiskers show min and max (excluding outliers defined as more distant to hinge than 1.5 interquartiles). Point and error bar indicates mean and standard error of the mean (95% threshold), respectively.

3.2. Microbial groups and plant strategies

3.2.1 Relative microbial PLFAs concentration

Overall, regardless of treatment, Gram+ PLFAs were the most abundant, with on average 31 ± 0.45 %mol PLFA, followed by Gram- PLFAs, who represented 22 ± 0.79 %mol PLFA. 18:1w7 (Zygomycota) was the most abundant fungal PLFA with 9.6 ± 013 %mol PLFA, followed by 16:1w5 (AMF) with 5.4 ± 0.25 %mol PLFA and lastly 18:2w6,9 (Ascomycota/Basidiomycota), with 2.2 ± 0.16 %mol PLFA (Figure 5). Gram+ PLFAs concentrations were negatively correlated to Gram– (R = -0.81, $p < 0.001$, Figure S5A), and Ascomycota-Basidiomycota (R = -0.38, $p < 0.05$), but positively correlated with Zygomycota (R = -0.34, $p < 0.05$). Gram– bacteria PLFAs were also negatively correlated with Zygcomycota (R = -0.51, $p < 0.001$).

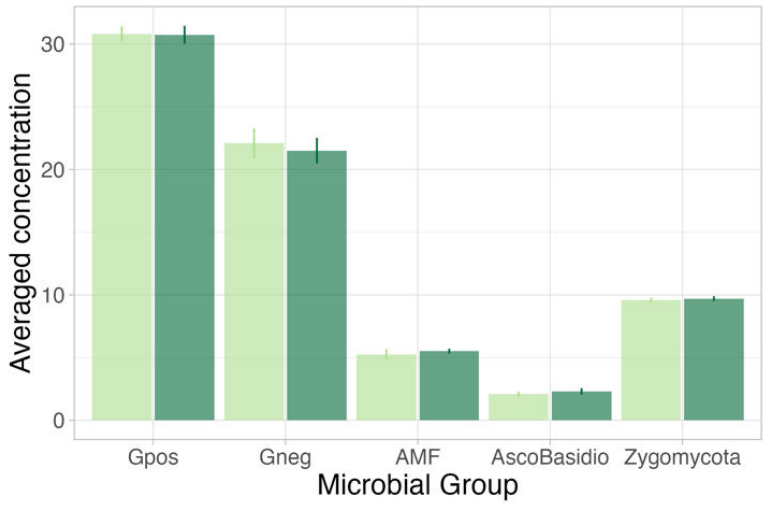


FIGURE 5 Averaged relative concentration (%mol) for different microbial groups across treatments

Plant-only (light green), and plant+litter (dark green). Error bar indicates standard error of the mean (95% threshold). The complement to 100% is unspecific microbial PLFAs.

Plant strategy and physiological traits were significant predictors for the relative abundance of two microbial groups out of five (Figure 6, Table S2). Zygomycota were positively associated (best model: R^2 = 0.40, weight = 0.13) with higher rhizodeposition (β_{RhSoil} = 0.65 ± 0.51, p < 0.05), and AMF were associated (best model: R^2 = 0.33, weight = 0.16) with higher %AMF colonisation ($\beta_{\%AMF}$ = 0.56 ± 0.34, p < 0.01) and with lower values on PCA1 (β_{PCA1} = -0.41 ± 0.35, p < 0.05). Gram+ bacteria were also associated to lower values on PCA1 (β_{PCA1} = -0.42 ± 0.36, p < 0.05, R^2_{adj} = 0.16). However, no model was able to satisfactorily predict neither Gram– bacteria nor Ascomycota/Basidiomycota (Figure 6, Table S4).

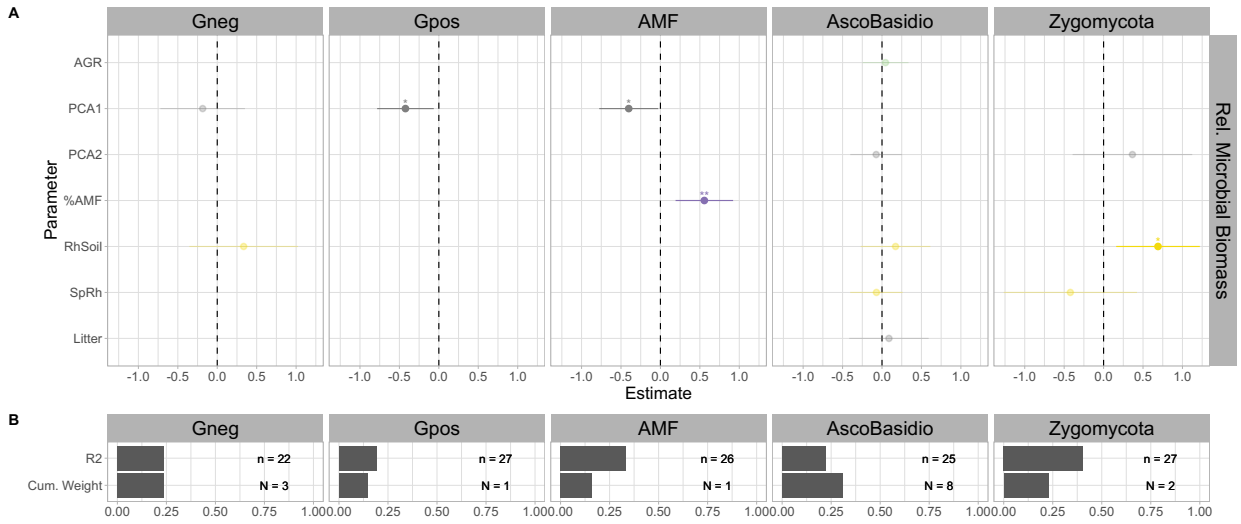


FIGURE 6 Model summary of microbial groups' relative concentration predicted by plant strategy

$$M = \beta_0 + \beta_{Nod}Nod + \beta_L L + \beta_{AGR}AGR + \beta_{PCA1}PCA1 + \beta_{PCA2}PCA2 + \sum_{PhT}\beta_{PhT}PhT + \epsilon$$

*Points indicate coefficient estimate, lines reflect 95% confident interval (CI), both are transparent if the CI intersect with 0. *: p< 0.05, **: p<0.01, ***: p <0.001. The R^2_{adj} of the best model (ΔAIC =0) and the cumulative weights of averaged models are reported in panel (B), with the sample size (n) and the number of models used for the averaging (N). If N =1, no averaging was performed. Gneg, Gpos, AMF and AscoBasidio refer to Gram+ bacteria, Gram– bacteria, Arbuscular Mycorhizal Fungi and saprotrophic fungi from the Ascomycota and Basidiomycota, respectively.*

3.2.2 Enrichment

All microbial PLFA were significantly enriched in ^{13}C compared to baseline (Figure 7) but Gram+ bacteria were less enriched (APE = 9 ± 1.4 ppm) than other groups, while AMF were more enriched (APE = 105 ± 29 ppm) than Gram– (APE = 45 ± 8 ppm) and 18:1w9 Zygomycota (APE = 51 ± 8 ppm). We did not perform statistical analysis on 18:2w6,9 Ascomycota/Basidiomycota, because they were detected by the GC-IRMS at only four points. Enrichment in all PLFAs tended to be positively correlated (Figure S4), except for Zygomycota who tended to be negatively correlated with AMF (R = -0.15, $p > 0.5$),

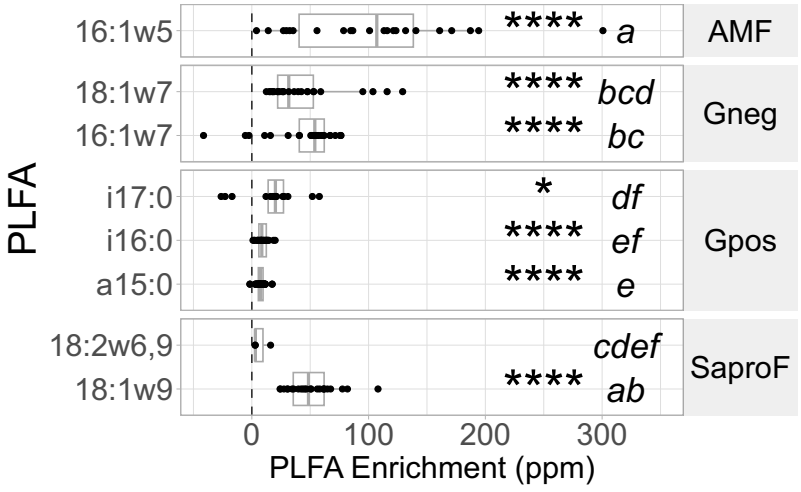


FIGURE 7 Enrichment of microbial PLFA, presented per microbial group.

*Difference with no enrichment (U Mann-Whitney test) is indicated by stars: *: p < 0.05, **: p < 0.01, ***: p < 0.001, **** p < 0.0001, while differences between groups (Wilcoxon test) is indicated by letters. Please note the low number of samples for 18;2w6,9 (n = 4). Boxplots show the median, as well as 1st and 3 quartiles (hinges), whiskers show min and max (excluding outliers defined as more distant to hinge than 1.5 interquartile range).*

and had no correlation with Gram–. APE of AMF and Gram– bacteria were the most strongly correlated with $R = 0.76$ ($p < 0.001$).

APE of microbial groups was relatively well predicted by our models, with best models' R^2 of 0.28, 0.46, 0.51 and 0.67 for Zygomycota, Gram+, Gram– and AMF, respectively (Figure 8, Table S3).

Rhizodeposition per gram soil was a strong predictor of enrichment across microbial groups, with a positive effect on all groups except Zygomycota ($\beta_{\mathrm{RhSoil}} > 0.5, p < 0.001$). The "DIY strategy", i.e., lower PCA1 values, were also associated with higher APE for AMF and Gneg, with β_{PCA1} = -0.43 ± 0.35 ($p <$ 0.05) and β_{PCA1} = -0.67 ± 0.39 ($p <$ 0.01), respectively. Specific root respiration was also a significant predictor of AMF's APE (β_{SpRR} = 0.38 ± 0.29, $p <$ 0.05).

Notably, microbial groups' APE showed far stronger variation than microbial groups' relative biomasses, with coefficients of variation (CV) ranging from 35 to 70% for the former, compared to 3-12.5% for the latter (excluding the group of Ascomycota-Basidiomycota from this comparison, as we had only four points for their APE, and because of the very small proportion of biomass, also had a notably higher CV).

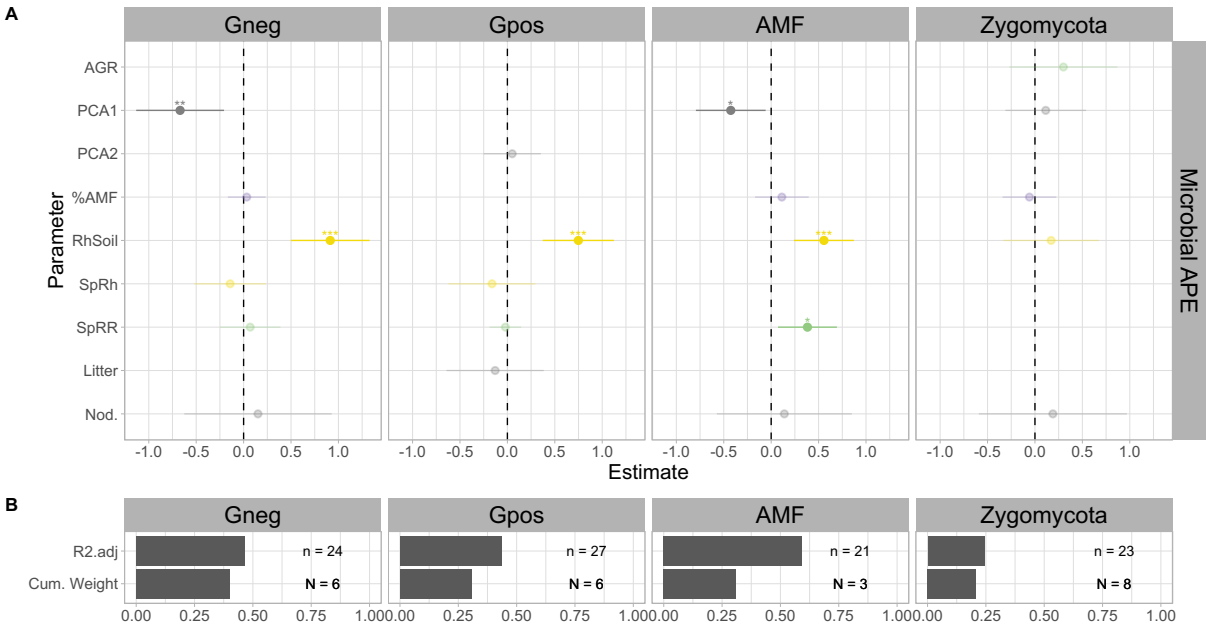


FIGURE 8 Model summary of microbial groups' enrichment predicted by plant strategy

$$M = \beta_0 + \beta_{Nod}Nod + \beta_L L + \beta_{AGR}AGR + \beta_{PCA1}PCA1 + \beta_{PCA2}PCA2 + \sum_{PhT}\beta_{PhT}PhT + \epsilon$$

*Points indicate coefficient estimate, lines reflect 95% confident interval (CI), both are transparent if the CI intersect with 0. *: p< 0.05, **: p<0.01, ***: p <0.001. The R^2_{adj} of the best model (ΔAIC =0) and the cumulative weights of averaged models are reported in panel (B), with the sample size (n) and the number of models used for the averaging (N). If N =1, no averaging was performed. Gneg, Gpos, and AMF refer to Gram+ bacteria, Gram– bacteria, Arbuscular Mycorrhizal Fungi and saprotrophic fungi from the Ascomycota and Basidiomycota, respectively.*

4. Discussion

Here, we showed that, in accordance with our first hypothesis, %AMF colonisation and root respiration did align with the 'outsourcing' strategy of the exploration gradient, and the acquisitive strategy of the fast/slow gradient, respectively, though the representation of the fast/slow gradient is blurred. Rhizodeposition, both per gram soil and per gram root was higher among legumes species, which are both acquisitive and outsourcing. Relative to our second hypothesis, we confirmed higher relative concentration of AMF PLFA under outsourcing species, and we found rhizodeposition per gram soil to be a good predictor of microbial enrichment in all groups except Zygomycota. We also demonstrated a shift towards outsourcing strategy with litter addition, with enhanced %AMF colonisation, associated with small increases in RCF, RMD and reduced SRL.

4.1. Clear exploration trade-off, but ambiguous fast/slow gradient

The exploration gradient, opposing species with high root diameter and species with high SRL was clearly apparent in our first PCA axis explaining 37% of variation. The picture is more complex for the second axis, which is based on the opposition between SLA and LNC against RDMC, analogous to root tissue density used in Weigelt et al. (2021). Indeed, this pattern looks like the fast/slow gradient, but RNC loads on the first axis as well, reflecting partial absence of orthogonality between both gradients. Even more importantly, if we consider AGR as the best representation of the fast-slow gradient (see for example Cardenas et al., 2021) then, PCA2 does not reflect our fast-slow gradient. Indeed, pots with high AGR are distributed all along the second axis. Such discrepancy is surprising but different elements (phenology and experimental conditions) might explain such apparent contradiction.

First, an effect of phenology on plant traits has been demonstrated, with younger individuals presenting more acquisitive traits that older ones (Barton, 2024; Garbowski et al., 2021; Mason et al., 2013). Thus, if conservative species were still in earlier developmental stages, it might explain the pattern we observed. However, two of our most conservative species, *Campanula rotundifolia* and *Galium verum* reached flowering in our experiment, and no plant was still in a juvenile stage at the time of the harvest, so it is unlikely that phenology alone would explain such a difference with expected patterns. Secondly, experimental conditions could also explain some deviation to the expected relationship between acquisitive attributes and high growth rates: as our soil was relatively rich, conservative species may have benefitted from nitrogen luxury consumption. Indeed, LNC and RNC showed one of the strongest trait variation in response to fertilisation (Siebenkäs et al., 2015). Cardenas et al. (2021) also found, in a relatively poor soil, that acquisitive grass species had higher C:N ratio and lower LNC and RNC than conservative ones. Craine (2009) highlighted that not only species ranking based on LNC varied across two experiments with different soil nitrogen content, but their relationships with leaf life span as well.

Perhaps more surprising is the absence of correlation between LDMC and RDMC, as both traits are supposed to be above/belowground analogous for organ lifespan. In our whole dataset, RDMC was moderately positively correlated with AGR, while high RDMC is supposed to be a conservative attribute, a relationship mainly found in forbs (not significant for other functional groups), and LDMC is supposed to reflect construction cost and slow growth better than other leaf traits such as SLA (Hodgson et al., 2011; Marino et al., 2010).

The absence of LDMC loading on PCA2 thus confirms the difficulty of interpreting it as the representation of the fast/slow gradient, and further justifies our choice to include AGR directly in the models.

4.2. %AMF colonisation and Specific Root Respiration align with expected strategies... (H1)

In accordance with our first hypothesis (H1.a), our models found that %AMF colonisation was relatively well explained by plant exploration strategy reflected by morphological root traits (PCA1), with higher RD and RCF promoting higher colonisation. Interestingly, %AMF colonisation was the trait most impacted by litter addition, with on average 60% more colonisation in presence of litter. As neither the effect of litter addition on AMF enrichment nor on rhizodeposition (either specific or per gram soil) were significant, this could mean that AMF directly benefited from litter addition, and not because the plant modulates its carbon allocation to AMF to promote litter decomposition. This is in line with Hodge et al. (2001) findings that the presence of a litter patch significantly promoted hyphal growth, with no detectable effect on plant growth, even though the plant did obtained nitrogen from litter decomposition.

Still conform with our expectations (H1.b), in our models, higher specific root respiration was associated with both higher AGR and higher values in PCA2 (high LNC, SLA). This is coherent with the meta-analysis of Han & Zhu (2021) presented in the introduction who found a positive correlation with RNC (high PCA2), and with the idea that more acquisitive species (defined here by higher AGR) have higher metabolic rates (reflected by higher specific respiration).

4.3. ... while rhizodeposition is primarily higher in legumes (H1)

Rhizodeposition was primarily explained by the ability to form nodules, that is, confounded with the legumes functional group. Legumes tended to have higher rhizodeposition, both per gram soil and per gram root, which is coherent with recurrent findings that legumes have higher rhizodeposition (Henneron, Cros, et al., 2020; Warembourg et al., 2003), though contrasting results also have been reported (e.g., in Williams et al. (2021), forbs displayed the highest specific exudation rate). Contrary to our hypothesis (H1.c), our model did not find strong links between rhizodeposition and plant economic strategy reflected by PCA axes, though the relations we expected were apparent in univariate relationships (positive correlation with AGR and PCA1): indeed, legumes possess both fast (higher LNC, RNC, high

photosynthesis rate) and cooperative (higher root diameter, lower SRL) attributes. On the other hand, specific rhizodeposition was negatively influenced by AGR, both according to our models and in univariate correlations. This leads us to a partial confirmation of H1.c, to which we attach the necessity for more investigation, clarifying different conceptions of rhizodeposition and of its position in plant economics space, independently from legumes.

Studies cited in the introduction used different measures of rhizodeposition. Henneron, Cros, et al. (2020) found higher rhizodeposition (per gram soil) to be associated with the acquisitive attributes and independent of the exploration gradient. Their estimation also includes root turnover rate, because of the continuous labelling. This probably reinforce the link to the fast/slow gradient, as acquisitive species should have higher turnover rate, thus leading in higher rhizodeposition, according to their definition. On the other hand, Guyonnet, Cantarel, et al. (2018) found, using a seven day labelling, a positive relationship between SRL and rhizodeposition (per gram soil). The species they studied were all grasses, which might suggest a powered relationship between the exploration gradient and rhizodeposition. A recent meta-analysis of extension of the root economics space (Matthus et al., 2025) may support this possibility, as root exudation was found to be associated with both ends of this gradient, though the number of studies including a estimation of rhizodeposition is very low (5). Interestingly, some demonstrated qualitative differences in exudation across functional groups, though low metabolite identification limits functional interpretation. Because of the large diversity of rhizodeposits (carbohydrates, amino-acids, various compounds involved in molecular dialogues such as flavonoids, P-mining compounds, etc.), the role of rhizodeposition may vary across functional groups, thus leading to a non-linear relationship with plant economics space dimensions.

4.4. Recent photosynthate allocation in microbial groups is more affected by plant strategy than microbial groups biomasses (H2)

Contrary to our second hypothesis, microbial community structure was only slightly affected by plant strategy. We found Zygomycota to increase with higher rhizodeposition per gram soil, and AMF to increase with %AMF colonisation, and to be associated with lower scores on PCA1, that is DIY species, grasses with high SLR values. These results must be interpreted carefully, as the models' residuals showed some heteroscedasticity despite our transformations. On the other hand, microbial group enrichment, was positively associated with rhizodeposition per gram soil for all groups except Zygomycota. In line with our hypothesis (H2.a), we found that enrichment in AMF PLFA tended to be higher with higher %AMF colonisation, but it was also associated with higher specific respiration and lower scores on PCA1 (high SRL grasses). The relationship with specific root respiration should not only be interpreted as plant economic strategy, as there are documented example of AMF enhancing root respiration (Wen et al., 2021). Interestingly, our may indicate that higher carbon exchange with the AMF is associated with higher root respiration, but whether this respiration reflects higher root respiration or higher AMF respiration cannot

be determined. On the other hand, the association with higher SRL grasses is surprising, because, even though the difference was not significant in our experiment, grasses have been found to have lower %AMF colonisation than other functional groups in field experiments, but not in greenhouse experiment (Šmilauer, Košnar, et al., 2020). Their AMF also have lower hyphal production efficiency (Gui et al., 2018), and a potentially higher foraging speed but lower foraging precision – based on the comparison between *Anthoxantum odoratum* and *Plantago lanceolata* (Šmilauer, Šmilauerová, et al., 2020). The strong correlation between the enrichment of AMF and Gram– bacteria is also apparent in our models, as they are both affected by the same attributes (high rhizodeposition per gram soil and low values on PCA1). It may also suggest that Gram– enrichment is partly due to the Gram– from the hyphosphere.

The fact that Zygomycota biomass but not enrichment was associated with rhizodeposition per gram soil may be evidence of their participation to the priming effect, with rhizodeposits stimulating their acquisition from SOM-derived carbon (Shahzad et al., 2015).

4.5. Litter addition affects the expression of root traits but not microbial communities

We expected litter addition to favour saprotrophic fungi and Gram+ bacteria over other groups, but we found no effect on fungal biomasses nor enrichment. However, litter addition had a significant impact on plant growth and root morpho-chemical traits, promoting higher growth rate, more cooperative attributes (higher %AMF colonisation, root cortex fraction and lower SRL) and more conservative attributes (higher RDMC and lower RNC) as well. The large difference of range between coefficient of variation and response ratio between traits underlines that some traits may be much more variable in response to environmental conditions (like %AMF) than other (RNC, SRL). Range of intraspecific variability is beginning to be considered as a functional trait in itself[10] (see Šmilauer et al., 2021 for example, for a plant species' ability to reduce %AMF colonisation in response to nutrient surplus). The fact that different traits related to the same strategy (for example, %AMF, SRL and RCF) demonstrate different (intra and inter) specific variability may add complexity for disentangling traits syndromes and plant economic strategies, and highlight the importance of better consideration of the belowground trait variability in future studies, by including more often environmental treatments, such as different soil fertility or soil texture.

In a meta-analysis, AMF colonisation have been found to increase root C:N ratio, especially in grasses (Yang et al., 2023), which is in line with our finding of decreasing RNC with higher %AMF colonisation. Pang et al. (2023) also found higher root tissue density (analogous to RDMC) with mycorrhization. However, the extent to which this is due to changes in plant tissue or the presence of the hyphae, who have their own density and C:N ratio, is unknown.

[10] Though one might argue that this measure cannot be considered as a trait according to Violle et al. (2007)'s definition, as it need the reference to other individuals to be evaluated.

4.6. Experimental limits

We explore in the next paragraph several limits which might have impair the detection of stronger links between plant economic strategies and microbial communities' structure and enrichment – beside the amount of rhizodeposition. First, all the pots were made from the same soil, which explains relatively small variation between PLFAs concentrations across treatments and species. The duration of the experiment may be relatively small compared to the time plant may need to exert a strong influence on microbial community. Indeed, microbial community composition have been detected to persist up to decades in transplant experiment (Crowther et al., 2019). Climatic stress (heatwave during the last month of the experiment) may have exerted a strong selection pressure that outweighed the effect of plant strategy. These elements can also be advanced to explain the absence of litter addition effect on the microbial community.

5. Conclusions

Here, we aimed at assessing the relationship of three root physiological traits, (root respiration, %AMF colonisation and rhizodeposition) to plant economic strategies. Consistent with our expectations, we found that higher root respiration and higher %AMF colonisation were respectively associated with the fast and cooperative strategies. Rhizodeposition, both "total" (per gram soil) and "specific" (per gram root), was primarily explained by a plant ability to form nodules, i.e. by its affiliation to the legume functional group, which tend to have acquisitive and cooperative attributes. By including a litter-addition treatment, we were also able to skim over the question of intraspecific variability in the PES, highlighting the need for further study.

We also investigated relationships between plant economic strategies and microbial communities, and more precisely, plant C allocation to soil microbes by rhizodeposition. We showed some dependence of all microbial groups to rhizodeposits, especially strong for Gram–, AMF and Zygomycota. AMF fungi relative biomass was positively associated with degree of root colonisation but also with DIY strategy, but their enrichment was predominantly related to rhizodeposition per gram soil and root respiration. On the other hand, Zygomycota relative biomass but not enrichment was associated with rhizodeposition per gram soil, which may suggest priming.

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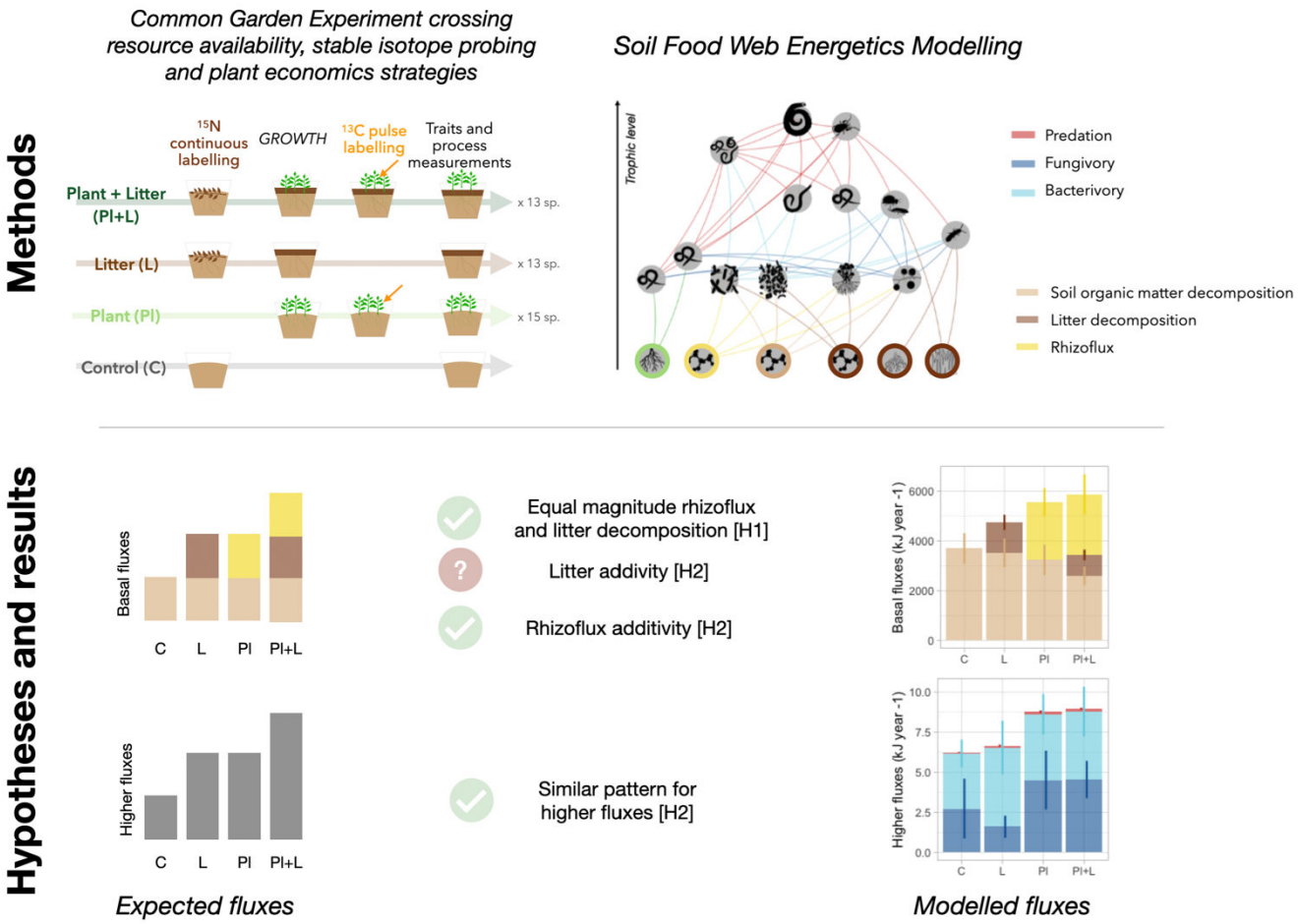
Chapter 2

Partitioning the importance of rhizodeposition and litter for soil food webs across 15 plant species with contrasting economic strategies[11]



[11] This article was submitted in *Functional Ecology* on March 5th, 2025.

Abstract

Biotic interactions are major drivers of ecosystem functioning, and many ecosystem functions are supported by trophic interactions. Quantification of energy fluxes in soil food webs thus offers a promising perspective to explore the relationship between trophic interactions and ecosystem functions. The quantity and nutritional quality of plant-derived resources at the base of food webs can influence soil community structure, and the way energy flows through the soil food web. However, contributions of litter and rhizodeposits are challenging to disentangle. Plant resource economic strategies are known to drive the quantity and quality of resources, but how they affect soil food webs remains elusive so far.

We applied a food web energetics approach to a mesocosm experiment manipulating the presence/absence of ^{13}C pulse-labelled living plants and ^{15}N continuously labelled litter for fifteen herbaceous plant species with contrasted economic strategies. This allowed us to investigate the relative importance of living roots and plant litter for the soil food web and how the food web energy fluxes were influenced by plant economic strategies.

Despite different pool sizes, energy fluxes from litter and rhizodeposition had the same magnitude. Our results highlight the positive effect of living plants on fungivory, carnivory and total fluxes, whereas plant presence decreased soil organic matter decomposition. In addition, the decomposition of litter and soil organic matter shifted from fungal to bacterial dominated fluxes in the presence of plants, whereas the fungal energy channel was dominated by fluxes from rhizodeposition. We found that litter phosphorus content was a good predictor of basal fluxes, with higher litter phosphorus content leading to higher litter decomposition and rhizoflux, but lower SOM decomposition. Higher growth rate of plants was associated with higher total fluxes, while root respiration positively affected litter decomposition, underlining the relevance of plant economic strategy as a predictor for plant species effects on soil food web functioning.

1. Introduction

Biotic interactions have been highlighted as key drivers relating biodiversity to ecosystem functioning (Bardgett & Wardle, 2010). Plants are an essential node in these biotic interactions. As primary producers, they incorporate external energy into the ecosystem and dispatch it belowground as plant-derived resources, supplying food to herbivores with living tissues, to detritivores with dead biomass, hereafter called litter (Cebrian & Lartigue, 2004), or to rhizosphere-associated organisms through rhizodeposition, *i.e.,* the release of organic compounds by living roots into the soil (Pausch & Kuzyakov, 2018). Plant species identity and strategy strongly influence plant-derived resources through different functional traits, which can complexify our understanding of plant influence on soil food webs (Wardle, 2004). However, there is no consensus about how plant traits and associated changes in resource quality and supply influence soil food web attributes and energy fluxes, particularly in the context of linkages between terrestrial above- and belowground compartments.

The plant economics space (PES), a theoretical framework based on functional traits involved in the acquisition, processing, and conservation of resources, allows us to go beyond a taxonomic approach for understanding the effects of plant species on soil food webs. It describes plant economic strategies according to two trade-offs (Weigelt et al., 2021). The 'fast-slow trade-off' reflects the compromise between (a) the fast-growing strategy (acquisitive species) supported by organs with high metabolic rate but short life span and (b) the slow-growing strategy (conservative species) characterised by investment in more resistant but less metabolically efficient organs, with lower nitrogen concentrations and higher dry matter content (Reich, 2014). The 'exploration trade-off' describes the compromise between (a) a plant investing in its own root system to explore the soil volume – the 'do-it-yourself' strategy –, opposed to (b) outsourcing soil exploration to arbuscular mycorrhizal fungi, the 'collaborative strategy', reflected by shorter and thicker roots, as well as a higher proportion of mycorrhizal colonisation (Bergmann et al., 2020). Traits used to characterise plant economic strategies are tightly linked with the quantity, quality, and localisation of the plant-derived resources in soil. Indeed, faster growing species tend to produce litter and roots of higher nutritional quality for decomposers – that is, richer in nutrients and poorer in secondary metabolite (Freschet et al., 2012, 2013) –, and to feature higher rhizodeposition rates (Henneron, Cros, et al., 2020; Kaštovská et al., 2015; Williams et al., 2022).

Quantity, quality and type of resources delivered by plants have been shown to shape both microbial (de Vries et al., 2012) and animal communities (Fujii et al., 2020; J. Zhang et al., 2022). For example, plant litter has long been recognised as an important driver of plant species' effects on soil food webs and processes (Hobbie, 2015; Wardle, 2004). Soil food web components respond to varying litter quality (Fujii & Takeda, 2017; Sauvadet, 2016): litter physical and chemical properties have been shown to drive the structure of soil fauna community (Raymond-Léonard et al., 2018; Sauvadet et al., 2017) and to influence demographic parameters of soil mesofauna such as springtails (Argote et al., 2023). Furthermore, soil food web

regulatory mechanisms, such as the relative importance of top-down *versus* bottom-up effects are modified by litter quality (Aupic-Samain et al., 2019; Lenoir et al., 2007), illustrating the importance of adopting a holistic food web perspective. However, the influence of plant traits on soil food web energy fluxes within the PES framework remains largely unexplored, even more so when considering plant belowground strategies and their influence on dispatched resources. For example, root nitrogen content may depend on the mycorrhizal status of the plant and its functional group, but also on its position within the fast-slow trade-off, as acquisitive species usually have a higher tissue nitrogen content. A few studies have begun to shed light on the relationships between root attributes and soil biota (Brousseau et al., 2025). Root traits have been shown to shape microbial communities (De Long et al., 2019), with more acquisitive species promoting bacteria over fungi, in particular Gram negative (Gram–) bacteria (X. Wan et al., 2021). Nematode trophic groups also seem to respond to specific root traits (Otfinowski & Coffey, 2020). For instance, herbivores tend to benefit from higher N content, while omnivores and predators profit from higher specific root length (J. Zhang et al., 2022).

Yet, these studies do not explicitly consider rhizodeposition, despite ample evidence for the critical importance of root-derived carbon from recent photosynthates for soil food webs (Fujii et al., 2016, 2021; Pollierer et al., 2007). Rhizodeposition is a readily available basal resource and does not require investment in exoenzyme production compared to soil organic matter (SOM) and litter consumption. The major contribution of rhizodeposits as a basal resource is to put in perspective with its small pool size. Explicit evaluation of the magnitude of their incorporation in soil food webs compared to litter and SOM are scarce (Pausch et al., 2015), partly due to difficulties to sample and analyse rhizodeposition in a living soil including soil biota (Oburger & Jones, 2018).

Partitioning the relative importance of litter and rhizodeposition and the energy channels they fuel is one of the major challenges left in this field of research (Brose & Scheu, 2014; Crotty et al., 2012; Pollierer et al., 2009). Among various competitive views of soil food web compartmentalisation, one can distinguish an herbivore path often called the "green channel", based on living plants and a detritivore path called the "brown channel" based on detritus, old stabilised rhizodeposits and microbially processed materials. Both channels are assumed to be united in higher trophic levels (Hunt et al., 1987). In this approach, rhizodeposits – here understood as all organic inputs from living roots into the soil, including direct inputs as well as inputs through arbuscular mycorrhizal fungi (AMF) – are largely ignored. They could be classified either as a part of the brown channel, considering it is a non-living, very labile pool of SOM (Moore et al., 2004) or as part of the green channel because it is living root-derived carbon from recent photosynthates (de Vries & Caruso, 2016; A. M. Potapov et al., 2024). Here, to emphasize their association with living plants, we include rhizodeposits in the green channel, hereafter termed living root-based channel, as opposed to the detrital "brown" channel.

While the opposition between fungal and bacterial channels was first described within the brown channel (Hunt et al., 1987; Moore & Hunt, 1988), root exudates have since been shown to be an essential resource for soil organisms (Li et al., 2021; Pollierer et al., 2007). These fluxes from recent photosynthates are likely mainly transferred to higher trophic levels through both bacteria and fungi. Even though the traditional concept of fungal/bacterial compartmentalisation may be too simplified (Geisen, 2016), it is likely that bacterial and fungal uses of this resource differ, as these groups have inherent functional differences such as contrasted morphology, carbon use efficiency and turnover rates (Waring et al., 2013). Furthermore, bacterial and fungal functional groups also differ in their affinity for root exudates (Ling et al., 2022; Treonis et al., 2004). Therefore, investigating more detailed microbial groups including Gram+ and Gram– bacteria, as well as saprotrophic and AM fungi, could be essential to progress toward a better understanding of the compartmentalisation of channels associated with basal resources in soil food webs.

Here, we adopt a food web energetic approach to quantify trophic functions such as herbivory, bacterivory, and fungivory. In this approach, energy is considered as a unifying currency to analyse the relationship between food web dynamic and ecosystem functioning, integrating concepts from network theory, metabolic ecology and ecosystem ecology (Barnes et al., 2018; Jochum et al., 2021). To explore the relative importance of litter and rhizodeposition for energy fluxes into soil food webs and how it is modulated by plant economic strategies, we conducted a common garden microcosm study manipulating the presence/absence of living plants and litter for 15 grassland species with contrasted economic strategies. We combined a novel food web energetics approach (Barnes et al., 2018; Jochum et al., 2021) with differential pulse labelling of living plants and litter with stable isotopes (^{13}C, ^{15}N), allowing to quantitatively trace energy fluxes from distinct plant-derived resources through different compartments of the soil food web, including both microbes and fauna (nematodes and microarthropods). We hypothesised that (i) rhizodeposition and litter support two relatively distinct energy channels of comparable magnitude. Assuming the channels are largely separate, we further hypothesized that (ii) the presence of each resource (rhizodeposition and litter) independently leads to higher fluxes in soil food webs, *i.e.* additivity of the living root-based and detrital channels. We also expected (iii) the presence of each resource to induce variations in the relative importance of fungal and bacterial channels, with fungi increasing in the presence of litter and bacteria being more closely associated to rhizodeposition. Finally, we hypothesized that (iv) plant economic strategy will impact soil food web energy fluxes, with acquisitive plant species being associated with higher fluxes and greater bacterial over fungal fluxes, while outsourcing plant species promote higher energy fluxes to AMF.

2. Materials and Methods

2.1. Experimental design

2.1.1 Set-up

We selected fifteen grassland plant species from three functional groups (legumes, graminoids, and forbs). Species selection was based on trait values from the literature to cover the fast-slow trade-off across the five species within each functional group and the exploration trade-off overall (Table S1.1). For each species, two factors were crossed: (i) living plant presence/absence (monoculture) and (ii) plant litter presence/absence (shoot and root), with three replicates for each of the three treatments, except for control treatment (absence of both living plant and litter), for which we had six pots in total. Plants provided resources through the 'living root channel' – rhizodeposition and living root tissue –, while the "detrital channel" was always present at least with SOM, with or without litter.

Litter of each species labelled with ^{15}N (10 atom%) was produced under hydroponic conditions (Supp. Mat. §1.2.1). Subsamples of above- and belowground litter were analysed to characterise elemental contents (Mn, K, Mg, Ca, P) with an ICP spectrometer (iCAP 7000 Series, Thermo Fisher Scientific), except for C and N, assessed using an elemental analyser (Flash, 2000; Thermo Fisher Scientific, Cambridge UK). Due to insufficient biomass production, *Campanula rotundifolia* and *Nardus stricta* species were excluded from the litter addition treatment.

The pots were handled in three blocks, each containing one replicate of the 15 species for plant-only treatment, 13 species for plant+litter treatment, 13 species for litter-only treatment, and 2 control pots with only soil – 129 pots, total. 6-L pots (22 cm deep, 20.75 cm mean diameter) were filled at 0.8 $g \cdot cm^{-3}$ with soil collected in a permanent urban mesophilic grassland (0-20 cm depth) at 49°28'28.3"N 1°04'17.6"E in Mont Saint-Aignan (France) after 5 mm sieving, during which all visible macroinvertebrates were removed. For the litter treatment, root litter (0.7 $g \cdot pot^{-1}$) was incorporated into the first 7 cm, while shoot litter (1.5 $g \cdot pot^{-1}$) was deposed on the surface and sprinkled with the first soil centimetre to prevent wind scattering. Litter application amounts were calculated based on grassland plant productivity, detrital production, and biomass allocation from data available in the literature. To avoid biased litter availability compared to living plants, we also adjusted the amounts according to pot density (Supp. Mat. § 1.2.2).

Seedlings of each of the 15 species germinated until 2-leaves stage and then preserved at 4°C to synchronise the species before transplanting seven individuals per pot on June 10th, 2022. Dead seedlings were replaced until the fifth week after transplantation. Plants were grown for three months in an outdoor experimental garden at 49°27'27.9"N 1°04'06.0"E, in Mont-Saint-Aignan (France). Soil moisture was kept above 60% of field capacity using automated watering, supplemented, if necessary, by weekly hand-watering based on pot weight.

2.1.2 ^{13}C pulse labelling and plant traits

Photosynthesis was measured before harvest in the 11th week of growth on *in situ* leaves with a LI-6400 (LI-COR Biosciences) assessing net CO_2 assimilation. Measurements were performed on 1 to 10 leaves per pot, combining leaves from up to two individuals when possible. The measured leaves were then cut and scanned within 24h after harvest (conserved at 4°C) using an Epson Expression LA2400 scanner coupled to WinRhizo Pro 2020 to assess leaf area.

Plant ^{13}C pulse labelling was conducted in September 2022. Due to the high number of pots, we processed one block (43 pots) per week. At the beginning of each week, the 28 pots with living plants were pulse-labelled with ^{13}C-enriched CO_2 (10 atom%) at 750-900 ppm during two consecutive days for 6 hours in a 2 m^3 hermetic chamber linked to a LI-830 CO_2 analyser (LI-COR Biosciences) according to Pang et al. (2021, Supp. Mat. § 1.3.1). Photosynthetically active radiation in the labelling chamber, measured with a LI-6400, ranged from 100 to 250 µmol m^{-2} s^{-1} at various heights, which is significantly lower than natural light but typical for growth chamber experiments (Belluau and Shipley, 2018; Shipley, 2006).

On the third day after the start of the labelling, pots were harvested. Total above-ground biomass was clipped at 1 cm above ground and dried at 35°C for 48h. Root traits were measured on fine roots collected by three 14 cm deep core samples at the barycentre of three plants within each pot, excluding tap roots. Fine roots' respiration rate was measured within 10 hours after sampling using a Li830 CO_2 analyser coupled to a chamber kept at 23°C within a bain-marie device. Samples were acclimated in the bain-marie for 5 minutes prior to measurement according to Lak et al. (2020). AMF colonisation was determined over 10 points on 10 dried fine root fragments of 1 cm at x200 magnification, according to McGonigle et al. (1990). Total root biomass was sorted from the pot after the last week of harvest, water washed and dried at 35°C for 48h before weighting.

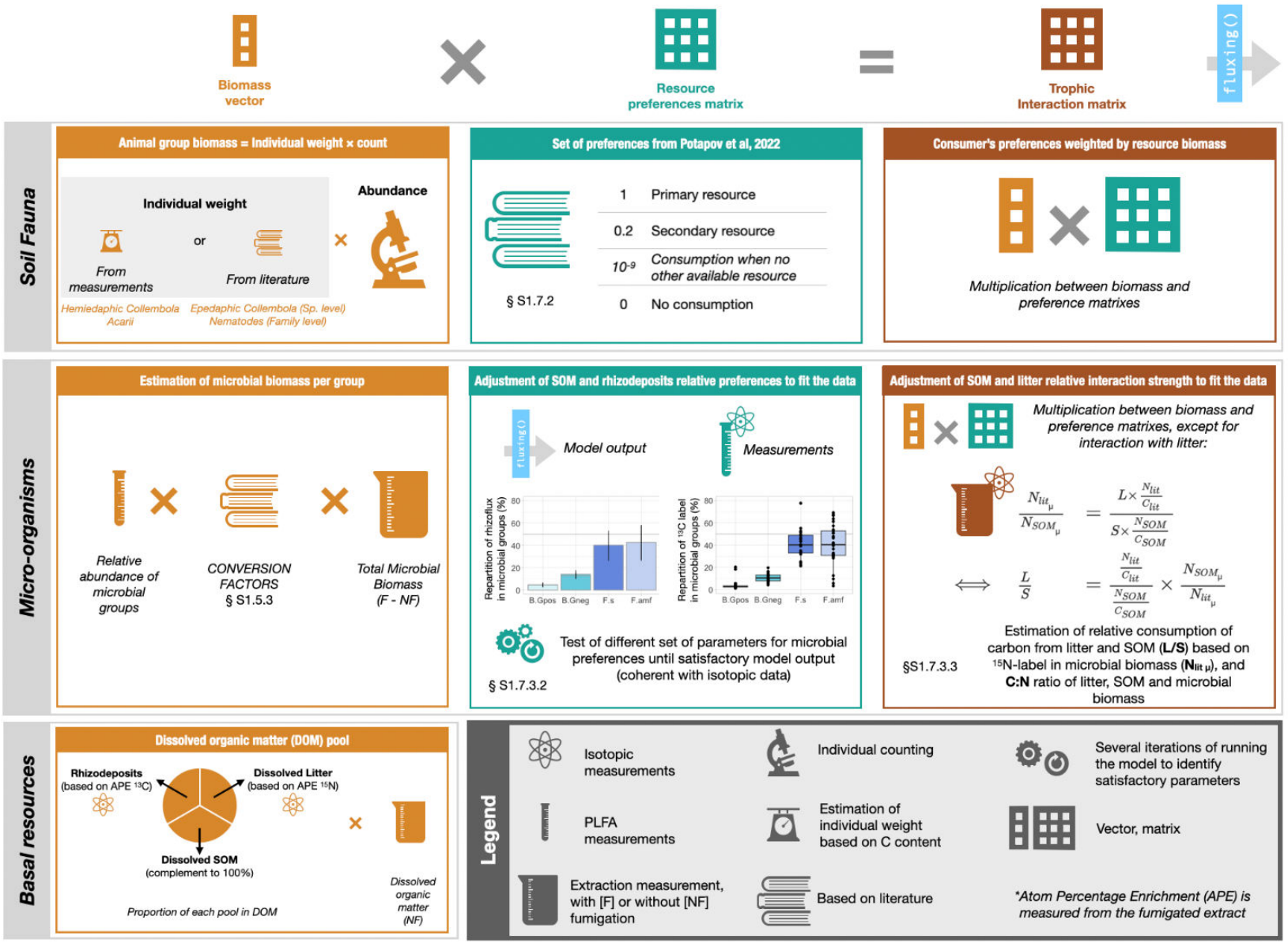


FIGURE 1 Overview of the construction of the trophic interaction matrix.

§S1.5.3, §S1.7.2, §S1.7.3.2, and §S1.7.3.3 refer to sections in the supplementary material & methods.

2.2. Food-web energetics approach

Energy fluxes in the soil food web were calculated based on steady-state food web modelling, which assumes that energetic demand of each node is met by energy uptake from lower trophic levels, taking into account losses during assimilation. Energetic demand includes metabolic rate and consumption by higher trophic levels (Potapov et al., 2024). Fluxes (F) to each consumer node were calculated according to the following formula (Barnes et al., 2018):

$$F = \frac{1}{e} \cdot (X + L)$$

where e is diet-specific assimilation efficiency, X is the summed individual metabolic demands within the node and L the loss of energy to higher trophic levels via consumption. Flux is then partitioned between the resource nodes according to the trophic interaction matrix, i.e. resource preference matrix weighted by resource availability based on biomass (see Figure 1 for an overview, Supp. Mat. §1.7.1).

2.3. Characterisation of soil food web components and their interactions

2.3.1 Basal resources

Basal resources were separated into two items, accessible to (i) fauna (litter, roots) and (ii) to microbes, which absorb only dissolved molecules. Living root biomass was estimated from fine root density, since phytoparasites and facultative phytophagous nematodes are more likely to feed on fine roots than tap roots. Litter available for detritivorous microarthropods corresponded to the initial input of litter.

We used the dissolved organic matter (DOM) pool to assess the relative abundance of rhizodeposits, litter and SOM pools for microbial feeding (Supp. Mat. § 1.4). We estimated SOM-derived resources in the DOM by subtracting proportion of carbon from rhizodeposition and litter from total DOM. Due to the absence of ^{13}C signal in DOM, attributed to the sampling time (12h after the end of the labelling) combined with the very high turnover of rhizodeposits (< 1h for low molecular weight compounds; Boddy et al., 2007), we used microbial biomass ^{13}C enrichment corrected for labelling intensity (dependent on block, Table S1.2) as a proxy for the proportion of rhizodeposits in DOM. The estimation of litter-derived DOM pool size was based on the ^{15}N signal of DOM corrected for labelling intensity and litter C:N ratio (dependent on plant species, Table S1.3). Note that using the ^{15}N signal introduces some bias, as carbon and nitrogen have very different dynamics in the dissolved pool, especially in the presence of plants that take up nitrogen.

2.3.2 Microbes: Phospholipid fatty acid and metabolic quotients

Soil microbial parameters were measured on soil sieved at 2 mm from three 0-7 cm deep, 5 cm diameter core samples. Soil microbial biomass was determined by the fumigation-extraction method according to ISO 14240 (1997) modified using an extractant concentration of 0.2 mol · L^{-1} K_2SO_4 solution to facilitate

following isotopic measurement on lyophilised extracts (Makarov et al., 2015). Basal soil microbial respiration was assessed with a Li380 CO_2 analyser after a 24h-incubation at 23°C in airtight pots filled with CO_2-free atmosphere. Soil moisture was standardized at 60% ± 10% of water holding capacity before incubation.

The biomass of microbial trophic guilds was quantified using the phospholipid fatty acid (PLFA) method. Soil samples from the three replicates of each modality (intersection of species and treatment) were pooled, and PLFA analyses were restricted to these composite samples. The extraction and derivatisation were performed according to Frostegård et al. (1993). Concentrations of resulting phospholipid methyl esters were analysed using a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA). The ^{13}C isotopic signature was assessed at the Centre for Stable Isotope Research and Analysis (University of Göttingen) on a Thermo Finnigan Trace Gas Chromatograph coupled via a GP interface to a Delta V mass spectrometer (Thermo, Bremen, Germany, Supp. Mat. §1.5.1). PLFAs were assigned to microbial groups according to the classification of Joergensen (2022, Table S1.4), considering they represent different trophic guilds.

The biomass of each group was determined using specific conversion factors (Supp. Mat. § 1.5.3, Table S1.5-6). The microbial biomass of each group was calculated by multiplying the proportion of each group in the pooled sample by the pot's microbial biomass estimated by fumigation-extraction.

Metabolic quotient, calculated from soil respiration rate and fumigation-extraction microbial biomass, was corrected for mean temperature during the growth period (Xu et al., 2017; Supp. Mat. §1.6). It was then partitioned by relative biomass proportion, assuming that bacteria respire twice as much as fungi per unit biomass (Sakamoto & Oba, 1994, Supp. Mat., §1.6). In treatments without plants, AMF were assumed to be dormant, so their relative contribution to metabolic need were reduced by 0.001 (Lennon & Jones, 2011; Price & Sowers, 2004). Metabolic needs were then calculated by multiplying the metabolic quotient of a group by its biomass. Assimilation efficiency of microorganisms was set to one, reflecting their external digestion system.

2.3.3 Nematodes and microarthropods

Nematodes were extracted from 100 g of fresh soil from the 7-cm deep core in a Baermann funnel (McSorley & Walter, 1991) and counted while active under a stereomicroscope. After decantation, nematodes were fixed using a 4% formaldehyde solution and mounted on microscope slides. On average, 100 nematodes per mass slide were identified from each sample to the family level at 400 magnification (Bongers, 1988). We classified them into five trophic groups: bacterivores, fungivores, omnivores, predators and herbivores (Yeates et al., 1993). Individual fresh weight for each family was retrieved from the Nemaplex database (http://nemaplex.ucdavis.edu/).

Microarthropods were extracted from a 7 cm deep, 5 cm diameter core sample over 10 days, according to the dry-funnel method (Tullgren, 1918) and stored in 70% ethyl alcohol until separation under a stereomicroscope. Acari were identified to the order/suborder level, i.e. Mesostigmata (Gamasida), Cryptostigmata (Oribatida), and Prostigmata (Actinedida), using Coineau et al. (1997). Because of limited recovery of other groups, only Mesostigmata were considered afterwards. Collembola were identified to species level following several keys (Gisin, 1960; Hopkins, 2007), except for a few only identified to genus. All Collembola were assigned to a life form – i.e. epedaphic, hemiedaphic, euedaphic (Gisin, 1943) – representing dispersal ability and functional attributes such as reproduction, mobility, and metabolic activity (Chauvat et al., 2014; Coulibaly et al., 2019; Petersen, 2002). Euedaphic springtails were barely recovered and thus not included in further analysis.

For each group within each pot, i.e. predatory mites, epedaphic, and hemiedaphic springtails, a subsample of the collected individuals was analysed for ^{13}C isotopic signature with a Delta V Advantage Thermo Electron (Bremen, Germany) isotope ratio mass spectrometer (IRMS) and C content with a Euro EA 3000 EuroVector S.p. A (Milan, Italy) at the Centre for Stable Isotope Research and Analysis (University of Göttingen). For epedaphic springtails, individual mass was assessed from literature (Persson & Lohm, 1977; Petersen, 1975; Tanaka, 1970) for each species for both adults and juveniles, while biomass of predatory mites and hemiedaphic springtails was calculated based on C content measured on the EA-IRMS. Pots with no recovery of a faunal group were assigned a biomass of zero.

Metabolic needs were quantified at the individual scale using a model based on individual body mass, environmental temperature (Table S1.7), and phylogeny (Ehnes et al., 2011), and aggregated by trophic group. Assimilation efficiency was estimated from prey nitrogen content and calculated according to Jochum et al. (2017).

2.3.4 Resource preference and trophic interaction matrices

We used a resource preference matrix derived from Potapov et al. (2022) for faunal preferences of various food resources (Supp. Mat. §1.7.2). Briefly, it contains three levels of interactions: 1 for primary food source, 0.2 for secondary food source (consumed five times less than primary source), and 0 when there is no consumption. For microbial preferences, we started with a resource preference matrix based on the same rules, with rhizodeposition as primary resource for every microbial group, and SOM and litter as a secondary resource for all groups except AMF. This, the initial resource preference matrix was fine-tuned to align with our microbial isotopic signatures. Preferences of Gram– bacteria and saprotrophic fungi for SOM relative to rhizodeposition had to be reduced to 0.002, while preferences of Gram+ bacteria for SOM were set to 0.02 (Supp. Mat. §1.7.3.1, Figure S1.1). Relative interactions of litter and SOM consumption were scaled directly, using ^{15}N signature of microbial biomass, C:N ratios of litter, SOM, and microbial biomass (Supp. Mat. §1.7.3.2, Figure S1.2), thus bypassing the biased estimation of litter-derived carbon in the DOM pool. Trophic relationships are shown in Figure 1A. To limit self-

feeding/cannibalism, the diagonal of the resource preference matrix was scaled by 0.1 (Gauzens, 2024 - personal communication). The final resource preference matrix is available in Table S1.8 (Supp. Mat. §1.8).

2.4. Energy flux computation

Using the *fluxweb::fluxing* function (Gauzens et al., 2019), we calculated energy fluxes per square meter, scaling feeding preferences by resource availability (biomass preference parameter set to 'true'), metabolic losses defined at the node level (biomass losses set to 'false') and accounting for different absorption efficiency for microorganisms (efficiency level set to 'link specific'). Inputs values are detailed in Table S1.9 (Supp. Mat. §1.8).

Following Gauzens et al. (2019) we obtained trophic functions by summing up fluxes from roots, SOM, fungi, bacteria, litter and animals to their consumers to assess herbivory, SOM decomposition, fungivory, bacterivory, litter decomposition and predation, respectively. We also calculated the fluxes from rhizodeposits to their consumers, thereafter named 'rhizoflux'.

2.5. Statistical analysis

All analyses were conducted with R version 4.4.1. We removed extreme points (*sensu* $1^{st}/3^{rd}$ quartile +/– 3 times interquartile range) before statistical analyses to avoid skewing the mean compared to the median. These outliers, likely due to propagated measurement errors, accounted for a maximum of 3.9% of microbivory values and even less for other fluxes (Table S1.10-12). We explored the effect of resource addition, plant traits, and litter properties on node biomass, soil food web fluxes, and the ratio of fungal vs. bacterial channels (*f:b* channel ratios) with linear mixed models (LMM) with the package *lme4*.

Three models were tested for each flux, except herbivory where we only tested (1) and (2):

$$F \text{ or } f:b \text{ or } B = \beta_0 + \beta_L L + \beta_{Pl} Pl + \beta_{L\,Pl} L\,Pl + b_B B + b_{Sp} Sp + \epsilon \quad (1)$$

$$F = \beta_0 + \beta_{Pl} Pl + \sum_X \beta_X X + b_B B + \epsilon \quad (2)$$

$$F = \beta_0 + \beta_L L + \sum_X \beta_X X + b_B B + \epsilon \quad (3)$$

where F is a flux, *f:b* is a channel ratio, B is a node biomass, L is the presence/absence of litter, Pl is the presence/absence of plant, B is the block (random factor, 3 levels), Sp is the species (random factor, 15 levels) and X is a plant trait (continuous variable) amongst absolute growth rate, root respiration, photosynthesis, AMF colonisation, the capacity of a plant species to form nodules (nod) or a litter property amongst element content (Ca, K, Mn, P), and C:N ratio. β are the fixed-effects coefficients, b_B and b_{Sp} are the coefficients for the block and species random-effects, respectively, and ϵ are the residuals errors.

Models were computed using the *lme4::lmer* function on data sets previously z-scored scaled, allowing to compute standardised regression coefficients that can easily be compared (β). To improve residuals normality, variables were transformed using ln(x+1) or arcsin(x) for percentages before scaling. Confidence intervals were computed with the *stats::confint* function. Marginal (R^2m) and conditional (R^2c)

coefficients of determination for each model were calculated using the *MuMIn* package. R^2m is based on variance explained by fixed effect only, while R^2c is based on both fixed and random effects.

For each model except type (1), a selection based on the Akaike information criterion (AIC) was performed with the *MuMIn::dredge* function which tests all variable combinations. Models within two AIC-units of the best models were tested for collinearity between variables using the *car::vif* function, and those with variance inflation factors > 5 were removed. When there was more than one model left, we chose to display the one with the most coefficients, or the one with traits present in other models if there were the same number of traits. All are available as supplementary results in Table S2.2-3, as well as a correlation matrix of litter traits (Figure S2.1).

For fluxes, the first model was tested on the full data set to assess the effects of basal resources on soil food web functions. As the second and third models aimed at assessing the effect of plant economic strategy on soil food web functions, they were tested only for treatments containing plants or litter, respectively. One low extreme for SOM decomposition and total fluxes was removed after log transformation to improve normality of the residues. Likewise, *f:b* channel ratios models were tested either on the full data set ($f{:}b_{microbivory}$, $f{:}b_{SOM\ decomposition}$), or on treatments containing either plants ($f{:}b_{rhizoflux}$) or litter ($f{:}b_{litter\ decomposition}$).

Within the results section, means ± standard deviation ($\overline{x} \pm \hat{\sigma}$), or coefficients estimate and 95% confidence interval (CI $\beta = [\hat{\beta} \pm \frac{CI}{2}]$) are given.

3. Results

3.1. Node biomasses

Most of the node biomasses were affected by the treatment (Table S2.1). On average across all treatments, the largest basal resource pools (Figure 2B) were – if present – litter (55.4 $g \cdot m^{-2}$) and plant roots (52.8 ± 35.6 $g \cdot m^{-2}$; 30% higher in the plant+litter treatment compared to plant-only). Microbially accessible resources (DOM) amounted on average to 10.7 ± 4.3 $g \cdot m^{-2}$, largely dominated by SOM-derived material, which represented on average 80%, 90%, and 99% of this pool in the litter-only, plant+litter, and plant-only treatments, respectively. Litter-derived material accounted for 19 % and 7.5% of basal resources in the litter-only and plant+litter treatments respectively, while rhizodeposits constituted less than 0.2% of the dissolved organic matter in all treatments containing plants.

Microbial biomass was dominated by saprotrophic (48.9 ± 17.1 $g \cdot m^{-2}$) and AMF fungi (32.4 ± 11.4 $g \cdot m^{-2}$), while Gram+ and Gram– bacteria represented 19.0 ± 6.2 $g \cdot m^{-2}$ and 12.9 ± 4.3 $g \cdot m^{-2}$, respectively (Figure 2B). Saprotrophic fungi were positively affected both by litter and plant addition (β_{Pl} = [0.78 ± 0.25], β_L = [0.38 ± 0.25], R^2m = 9.6 %, Table S2.1), while AMF were positively affected by litter addition (β_L = [0.28 ± 0.01], R^2m = 1.3 %).

Bacterivorous nematodes represented more than 75% of the nematode biomass across all treatments, with on average 0.18 ± 0.32 $g \cdot m^{-2}$. Fungivorous nematodes had a mean biomass of 0.005 ± 0.009 $g \cdot m^{-2}$, being highest in the presence of litter (β_L = [0.42 ± 0.40], R^2m = 3.4 %). Omnivorous nematodes showed an average biomass 10 times higher in the absence of plants, with a mean biomass of 0.027 ± 0.043 $g \cdot m^{-2}$ for the control and litter-only treatments (β_P = [-0.87 ± 0.66], R^2m = 3.4 %). Predatory nematodes had a higher biomass in the litter-only treatment, 0.011 ± 0.045 $g \cdot m^{-2}$, compared to less than 0.006 in other treatments (β_L = [0.5 ± 0.83], R^2m = 17 %). They were absent in more than 80% of our pots, all treatments included, and completely absent from the control pots, probably due to the smaller size of this treatment (n = 6). Phytophagous and facultative phytophagous nematodes had abundances up to 10 times higher in the presence of plants, overall amounting for 0.008 ± 0.015 $g \cdot m^{-2}$ and 0.001 ± 0.001 $g \cdot m^{-2}$, respectively (Figure 2B).

Microarthropod biomasses were dominated by springtails, with epedaphic and hemiedaphic life forms representing 0.27 ± 0.28 $g \cdot m^{-2}$ and 0.28 ± 1.22 $g \cdot m^{-2}$, respectively, while predatory mites accounted for 0.04 ± 0.04 $g \cdot m^{-2}$ (Figure 2B). The biomass of epedaphic springtails and mites was 7 and 2 times higher, respectively, in modalities with plants (for epedaphic springtails: β_P = [0.74 ± 0.29], R^2m = 12.6 % and for mites: β_P = [0.43 ± 0.01], R^2m = 3.4 %), and the biomass of hemiedaphic springtails was higher in the plant+litter treatment than in all others (5.3, 2.3 and 1.7 times higher than litter-only, control and plant-only treatment respectively).

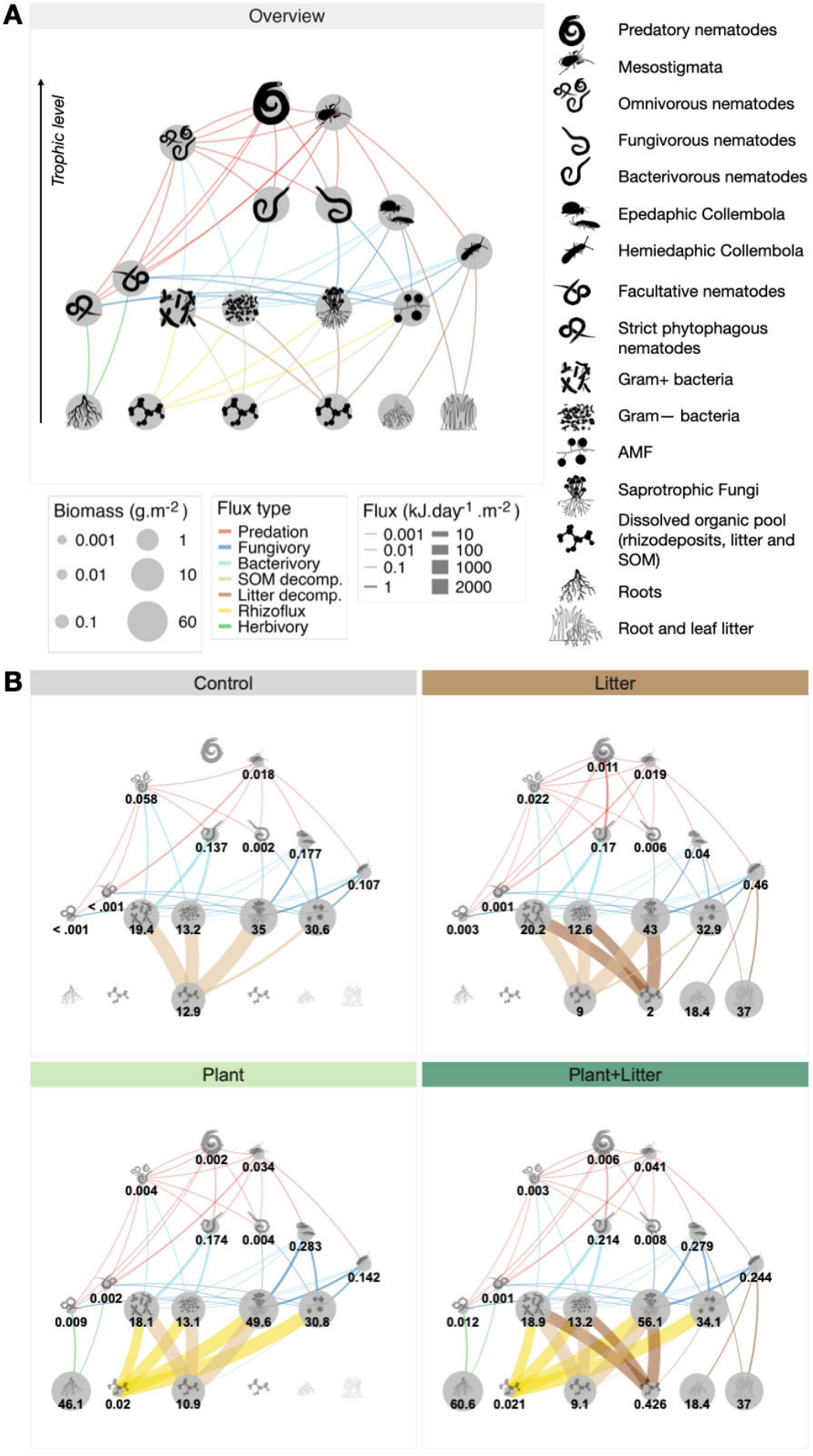

A
Overview
Trophic level
Predatory nematodes
Mesostigmata
Omnivorous nematodes
Fungivorous nematodes
Bacterivorous nematodes
Epedaphic Collembola
Hemiedaphic Collembola
Facultative nematodes
Strict phytophagous nematodes
Gram+ bacteria
Gram— bacteria
AMF
Saprotrophic Fungi
Dissolved organic pool (rhizodeposits, litter and SOM)
Roots
Root and leaf litter
Biomass (g.m-2)
0.001
0.01
0.1
1
10
60
Flux type
Predation
Fungivory
Bacterivory
SOM decomp.
Litter decomp.
Rhizoflux
Herbivory
Flux (kJ.day-1 .m-2)
0.001
0.01
0.1
1
10
100
1000
2000
B
Control
0.018
0.058
0.137
0.002
0.177
0.107
< .001
< .001
19.4
13.2
35
30.6
12.9
Litter
0.011
0.019
0.022
0.17
0.006
0.04
0.46
0.001
0.003
20.2
12.6
43
32.9
9
2
18.4
37
Plant
0.002
0.034
0.004
0.174
0.004
0.283
0.142
0.002
0.009
18.1
13.1
49.6
30.8
46.1
0.02
10.9
Plant+Litter
0.006
0.041
0.003
0.214
0.008
0.279
0.244
0.001
0.012
18.9
13.2
56.1
34.1
60.6
0.021
9.1
0.426
18.4
37

FIGURE 2 Overview of (A) our conceptual soil food web and (B) mean fluxes and biomasses across experimental treatments.

In Figure 2-B, point size reflects node biomass (also indicated below each node), linewidth reflects flux intensity, and line color refers to flux type.
Pictograms by Svenja Meyer (fungi, nematodes and mesostigmata), Louise Folacher (roots) and phylopic (Creative Commons Attribution License 'CC BY', source: https://www.phylopic.org/).

3.2. Energy fluxes across treatments

Total fluxes ranged from 894 kJ·day^{-1}·m^{-2} to 11,106 kJ·day^{-1}·m^{-2} and tended to be higher in treatments with plants (around 5700 ± 2000 kJ·day^{-1}·m^{-2}, compared to 4500 ± 2300 kJ day^{-1}·m^{-2} for control and 4700 ± 1300 kJ·day^{-1}·m^{-2} for the litter-only treatment (Figure 2B, Figure 3A). This was reflected by a strong positive effect size of plant presence ($\beta_{P/}$ = [0.64 ± 0.33], R^2m = 7.8 %, Figure 3B). SOM mineralisation was the largest flux in every treatment, representing 46.5 ± 9.0 %, 58.3 ± 9.2 %, 73.6 ± 11.1 % and 99.8 ± 0.12 % of plant+litter, plant-only, litter-only and control treatment, respectively. Both plant and litter presence had a negative impact on SOM decomposition ($\beta_{P/}$ = [– 0.73 ± 0.31], β_L = [– 0.61 ± 0.30], R^2m = 11.4 %). When present, fluxes from rhizodeposition contributed to total flux by around 40%, with 2300 ± 1400 kJ·day^{-1}·m^{-2}, and we found no differences between treatments. Litter decomposition represented 14.7 ± 5.8 % of total fluxes in the plant+litter treatment and 26.2 ± 11.1 % in litter-only, with a 30% decrease in the presence of plants. This was reflected by a small effect size in our model (CI $\beta_{P/}$ = [– 0.12 ± 0.04], R^2m = 13,6 %). Herbivory was very low compared to other fluxes from basal resources, accounting for only 0.3 kJ·day^{-1}·m^{-2}, i.e. less than 0.01% of total fluxes, tending to be lower in the presence of litter (CI β_L = [– 0.32 ± 0.46], R^2m = 2.4 %).

Among fluxes to higher trophic levels, microbivory was most the prominent, divided into bacterivory (4.4 ± 2.9 kJ·day^{-1}·m^{-2}), which was stable across treatments, and fungivory, which was almost twice higher in the presence of plants (4.5 kJ·day^{-1}·m^{-2}, compared to 2.7 ± 3.7 % and 1.6 ± 1.4 % in the control and litter-only treatment, respectively). The variation of fungivory was reflected in the very strong positive effect size of plant presence (CI $\beta_{P/}$ = [1.15 ± 0.34], R^2m = 26.0 %). There were increased predation fluxes in the presence of litter (+70 %) and living plants (+140 %), reflected for the latter by a strong effect size of plant presence (CI $\beta_{P/}$ = [0.47 ± 0.4], R^2m = 4.2 %), although the model had very low explanatory power.

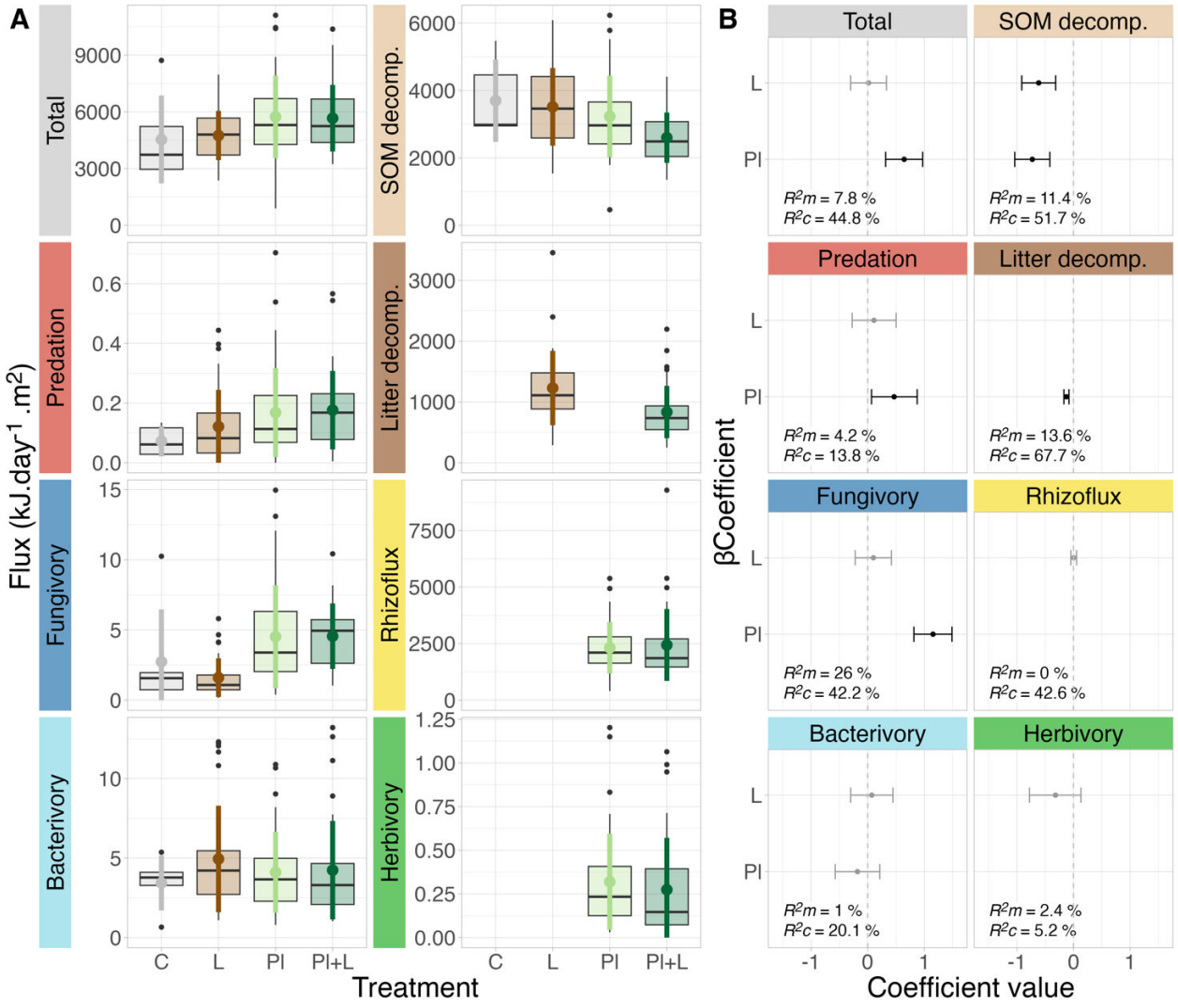


FIGURE 3 Effect of plant and litter addition on (A) energy fluxes across the four treatments and (B) coefficients associated with plant and litter presence for model referred to as (1) in the Materials & Methods section.

In panel A, the boxplots show the median, as well as 1st and 3 quartiles (hinges), whiskers show min and max (excluding outliers defined as more distant to hinge than 1.5 interquartiles), while point and line show mean and standard-deviation, respectively. C: control, L: litter-only, Pl: living plant-only, Pl+L: litter and living plant. In panel B, the point shows the estimated coefficient for LLM on standardised datasets, while error bars display the 95% confidence interval (CI), in black if the CI does not contain 0. Absence of coefficient indicates that the coefficient was not relevant (e.g.: β_{Pl} for herbivory. β_{Pl} and β_L are the coefficients associated with plant and litter presence, respectively. R^2m and R^2c are marginal and conditional coefficients of determination, respectively.

3.3. Bacterial and fungal channels

The presence of plants reduced the relative importance of fungal vs. bacterial contributions to litter decomposition ($f{:}b_{litter\ decomposition}$) from 1.19 ± 0.13 to 0.76 ± 0.24 (CI β_{Pl} = [– 0.44 ± 0.07], R^2m = 56.2 %; Figure 4A). This was also the case for $f{:}b_{SOM\ decomposition}$, which decreased from 0.98 ± 0.05 to 0.66 ± 0.19 without litter, and from 1.20 ± 0.13 to 0.76 ± 0.24 in the presence of litter (CI β_{Pl} = [– 0.44 ± 0.07], R^2m = 57.9 %; Figure 4A). Litter addition increased $f{:}b_{SOM\ decomposition}$ from 0.98 ± 0.05 to 1.20 ± 0.13 in the absence of plants, and from 0.66 ± 0.19 to 0.76 ± 0.24 in their presence (β_L = 0.09 ± 0.06, R^2m = 57.9 %). On the other hand, the presence of plants increased $f{:}b_{microbivory}$ from 0.59 ± 0.73 to 1.39 ± 1.02

(CI β_{Pl} = [– 0.85 ± 0.36], R^2m = 13.4 %; Figure 4B), with no effect of litter addition according to our model selection. Fungi – including both mycorrhizal and saprotrophic fungi – were clearly dominant in the relative use of rhizodeposits relative to bacteria ($f{:}b_{rhizoflux}$), with a mean ratio of 4.96 ± 1.66, and this dominance tended to be strengthened by litter addition (CI β_L = [0.53 ± 0.62], R^2m = 2.5 %, Figure 4C). Both fungi and bacteria contributed less to SOM decomposition in the presence of plants; therefore, the variations in *f:b* channel ratios in the presence of plants were mainly driven by the higher variation between treatment of fluxes to fungi compared to fluxes to bacteria (Figure S2.2, §2.5). Rhizoflux represented on average more than 50 % of fluxes to fungi (half to AMF and half to saprotrophic fungi), but only 10 % of fluxes to bacteria.

Although springtails contributed less than 1% to litter decomposition, they did participate tremendously in fungivory (> 50% of the flux across all modalities, > 80 % in treatments with plants, Figure S2.3). It is interesting to note that label recovery in microarthropods was not affected by our treatments, but differed strongly between ecological groups (Figure S2.4). Epedaphic springtails were 3 and 7 times less enriched in ^{15}N than predatory mites and hemiedaphic springtails. Hemiedaphic and epedaphic springtails were 20% and 200% more enriched in ^{13}C than predatory mites, with a mean ^{13}C enrichment of 120 ± 169 ppm for

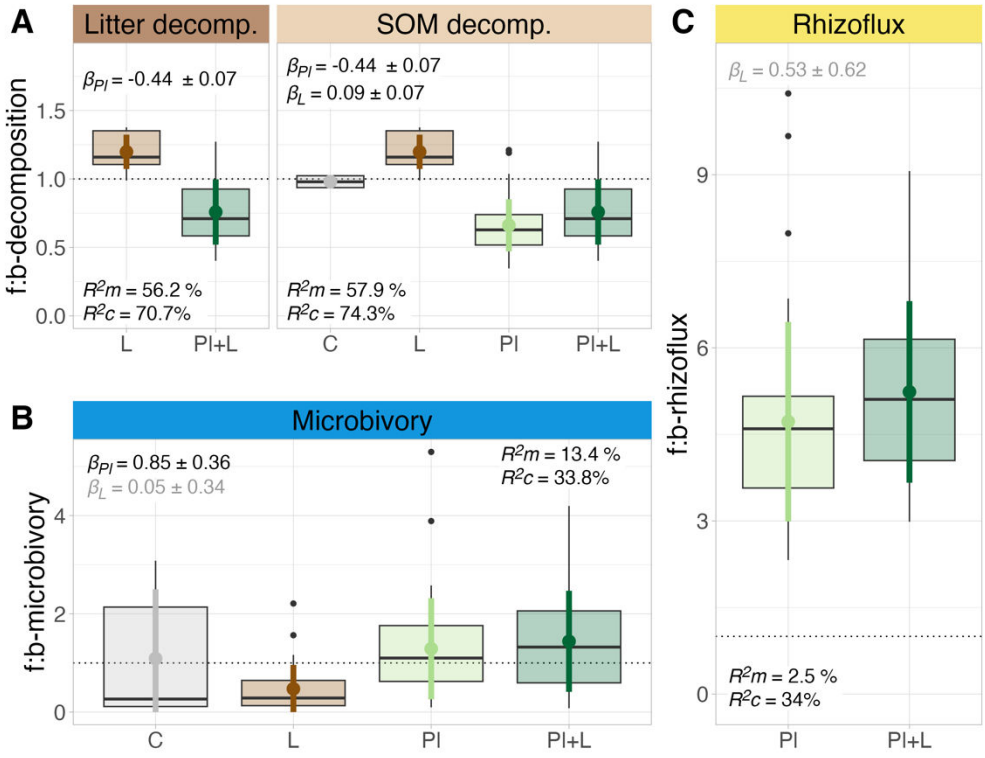


FIGURE 4 Relative contribution of fungal and bacterial channels (f:b) to litter and SOM decomposition (A), (B) microbivory and (C) f:b rhizoflux

C: control, L: litter-only, Pl: living plant-only, Pl+L: litter and living plant. Boxplots show the median, as well as 1st and 3 quartiles (hinges), whiskers show min and max (excluding outliers defined as more distant to hinge than 1.5 interquartiles), while point and line show mean and standard-deviation, respectively. β_{Pl} and β_L are the coefficients associated with plant and litter presence, respectively. R^2m and R^2c are marginal and conditional coefficients of determination, respectively.

epedaphic and 62 ± 59 ppm for hemiedaphic springtails. Bacterivory was dominated by nematodes, which contributed to more than 75% of the flux across all modalities (Figure S2.3).

3.4. Fluxes and plant economic strategies

Litter properties, in particular phosphorus content, were relatively good predictors for basal fluxes (Figure 5A), with R^2m of 16.5%, 13.8% and 33.3% for SOM decomposition, rhizoflux and litter decomposition, respectively. Litter phosphorus content had a strong positive effect on rhizodeposition (CI β_P = [0.38 ± 0.27], R^2m = 13.8 %), which was reflected in total fluxes (CI β_P = [0.19 ± 0.12], R^2m = 11 %) and a strong positive effect on litter decomposition (CI β_P = [0.51 ± 0.17], R^2m = 33.3 %), while it negatively impacted SOM decomposition (CI β_P = [– 0.19 ± 0.18], R^2m = 16.5 %). Litter decomposition was negatively affected by litter manganese content (CI β_{Mn} = [– 0.29 ± 0.17], R^2m = 33.3 %). Alternative equivalent models (ΔAIC < 2) included litter Mg content or C:N ratio for SOM mineralisation, and litter Mg and/or K content for rhizoflux (Table S2.2).

Plant strategy also showed explanatory power for energy fluxes (Figure 5B). Absolute growth rate (AGR) had a positive effect on total fluxes (CI β_{AGR} = [0.24 ± 0.22], R^2m = 5.3 %), and higher root respiration was associated with higher litter decomposition (CI β_{R_resp} = [0.6 ± 0.45], R^2m = 28.6 %). The ability to form nodules had a positive effect on rhizoflux (CI β_{nod} = [0.79 ± 0.45], R^2m = 14.0 %), and was associated with higher total fluxes (CI β_{R_resp} = [0.36 ± 0.43], R^2m = 42.5 %). It also negatively affected bacterivory (CI β_{nod} = [-0.75 ± 0.38], R^2m = 9.5 %). Although AMF colonisation did not influence rhizoflux itself, it was slightly positively correlated with rhizoflux going to AMF (R = 0.21, P = 0.097, R is Pearson's correlation coefficient).

Plant traits and litter properties also affected *f:b* channel ratios, with root respiration and ability to form nodules positively affecting $f{:}b_{\,rhizoflux}$, AGR positively affecting $f{:}b_{\,microbivory}$ and root respiration negatively affecting $f{:}b_{\,SOM\ decomposition}$ and $f{:}b_{\,Litter\ decomposition}$ (Table S2.4), while litter P content negatively affected $f{:}b_{\,rhizoflux}$ positively $f{:}b_{\,microbivory}$, and litter Mn and Mg content negatively affect $f{:}b_{\,SOM\ decomposition}$ and $f{:}b_{\,litter\ decomposition}$ (Table S2.5).

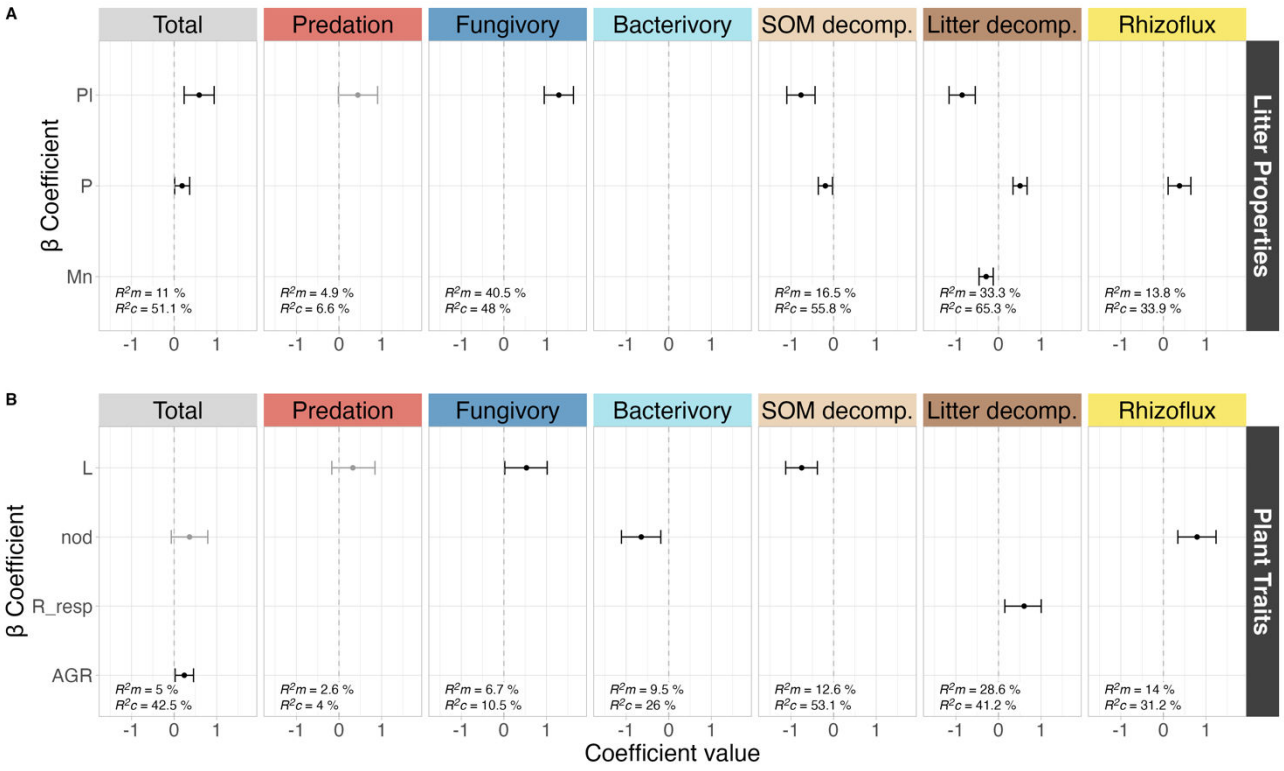


FIGURE 5 Standardised coefficients of linear mixed models explaining fluxes by (A) litter properties and (B) plant traits

The point shows the estimated coefficient of the model for the standardised dataset, while error bars display the 95% confidence interval (CI), in black if the CI does not contain 0. Absence of coefficient indicates that the coefficient was not relevant (e.g.: β_L for Litter decomposition) or not retained during model selection. β_{Pl} and β_L are the coefficients associated with plant and litter presence, respectively, while β_P, β_{Mn} are the coefficients for litter phosphorus and manganese contents, respectively. β_{nod} $\beta_{R_{resp}}$, β_{AGR} are the coefficients for capacity to form nodules, root respiration and absolute growth rate, respectively.

4. Discussion

This study is, to our knowledge, the first to apply the energy fluxes approach to soil food webs while in the same time partitioning rhizodeposition, litter, and soil organic matter based on isotopic labelling across multiple grassland species. We demonstrated, as we hypothesized i) that despite contrasting pool size, litter decomposition and rhizoflux had comparable magnitude, and that ii) rhizodeposition led to higher fluxes in soil food webs, highlighting additivity between fluxes from detrital and living root-based resources. We also highlighted the quantitative and qualitative impact of plant economic strategy on the soil food web, both on individual fluxes and *f:b* channel ratios.

4.1. Litter and rhizodeposition equally matter for belowground energy fluxes

In accordance with our first hypothesis, we found that, despite very different pool sizes, both rhizodeposition and litter decomposition fuelled energy channels of similar magnitude through the soil food webs. This is most probably explained by the high turnover rate of rhizodeposits, especially of low molecular weights exudates (Boddy et al., 2007), as they can be directly taken up by microbes, without the need for external digestion by exoenzymes. Rhizoflux was on average twice as high as litter decomposition. This is surprising, since gross rhizodeposition allocation represents only a fifth of allocation to plant biomass (Pausch & Kuzyakov, 2018), that will later enter the soil food web as detritus. Thus, even though rhizodeposits are supposed to be a resource of better quality compared to litter and SOM because of its direct availability, it seems unlikely that rhizoflux would dominate over litter decomposition in natural ecosystems, although it might vary seasonally. Moreover, in our experiment, since the estimate of litter microbial consumption is based on ^{15}N enrichment of the microbial biomass and not on C-dynamics, it neglects N absorbed by plants, likely leading to underestimation of litter decomposition in the plant+litter treatment. Detritivory represented only 1% of litter decomposition fluxes, and it would probably be higher in systems with macrofauna decomposers, such as woodlice and earthworms.

Interestingly, fluxes from litter to microbes were also independent of pool size: despite litter-derived DOM being twice as high in the litter-only as in the plant+litter treatment, the ^{15}N labelling in the microbial biomass was similar in both treatments. This decoupling between biomass (i.e., pool size) and fluxes was also evident in higher-order consumers. While fungal biomass was always higher than bacterial biomass, fungivory was only dominant in modalities including plants. The mechanisms for this decoupling are likely similar, as bacterial biomass is known to have a higher turnover rate than fungal biomass (Waring et al., 2013), and higher metabolic demands (Sakamoto & Oba, 1994). This suggests that fungal and bacterial channels are a relevant tool to study ecosystem functioning, even though they do not align with the separation of resources based on living roots and detritus. However, it may also be explained by higher biomass of epedaphic springtails in treatments with plants.

Furthermore, despite fine roots representing one of the largest pools, herbivory was negligible compared to the other basal fluxes. This – and low fungivory – may also be explained by the absence of K-strategists such as oribatid mites and euedaphic springtails, associated with more stable environments, that might not have had sufficient time for their establishment across the 3-month-growth period (Petersen, 2002).

4.2. Additivity of fluxes from detrital and living root-based resources across trophic levels

In line with our second hypothesis, we found additivity between fluxes from detrital and living root-based resources, demonstrating the importance and complementarity of these basal resources to sustain different pathways within the soil food web. As rhizoflux was not diminished by litter addition, and basal fluxes were two to three orders of magnitude larger than other fluxes, plant addition had a large positive effect on total fluxes. Additive effects were propagated across trophic levels, as indicated by increased fluxes through predation and fungivory in the presence of plants, suggesting that bottom-up control is the dominant structuring force in the food webs studied. In contrast, litter had a negative effect on SOM decomposition, suggesting the absence of additivity within the detrital channel – i.e., between SOM and litter. Instead, the apparent substitution between these two resources (SOM and litter) could indicate a negative priming effect reflecting microbial preferences for fresher organic matter (Bernard et al., 2022). Interestingly, plant presence had a relatively large negative effect on SOM decomposition, implying partial substitution/negative priming as well. These results could have important implications for the export of crop residues into the agroecosystem and require further research (Hedde et al., 2024; Mary et al., 2020). We also found a small negative effect of plant presence on litter decomposition which could be related to the same mechanisms, but it may also be an artefact linked to our model hypotheses.

The diminution of SOM decomposition in the presence of living plants may also be related to the dynamics of the microbial community. As the lower relative importance of fungi in decomposition is driven by saprotrophic fungi switching more from SOM to rhizodeposits than bacteria, it would be interesting to see if this is due to shifts in the fungal communities: as the classification based on PLFA analyses is very coarse, we would not have detected a change toward plant-parasite taxa among fungi that possess 18:2ω6,9 or 18:1ω9 PLFAs.

4.3. Fungal vs bacterial channels

The relative importance of fungal and bacterial channels for decomposition, usually based upon the fungal:bacterial PLFA ratio, is an indicator of ecosystem functioning. When comparing systems across anthropogenic land use gradients (X. Wang et al., 2019), higher ratios are associated with higher carbon storage in stable ecosystems, while lower ratios are related to faster nutrient and energy cycling (Frostegård & Bååth, 1996; Malik et al., 2016). The nematode-based channel index estimates the relative importance of each channel for higher trophic levels, thus reflecting decomposition pathways. It is usually expected

to coherently vary with the fungi:bacteria ratio (Ferris et al., 2001), in line with bottom-up regulation by resource quality (Ferris et al., 2001) or environmental influence on microbial groups, with more disturbed environments being associated with lower ratios (Zhang et al., 2016). Here, we show that while the fungivory:bacterivory ratio does follow bottom-up control expectations (increasing when total fluxes to fungi relative to total fluxes to bacteria increase), contrary to the nematode-based channel index, it does not reflect the relative contribution of microbial groups to decomposition.

We found that despite living plants led to increased fungivory, with higher biomass of springtails, the fungal was not lower compared to the litter-only treatment. This suggests that fungi (both saprotrophs and AMF) benefited from the addition of living root basal resources (e.g. rhizodeposits), but that additional fungal biomass was transferred to higher trophic levels via consumption by fungivores (springtails). Indeed, springtails were enriched in ^{13}C only two days after labelling, emphasizing their link to microbial groups associated with recent photosynthates. This supports recent findings showing springtails to be highly related to microbial groups (bacteria and/or fungi) associated with rhizodeposits across various land use types (Li et al., 2021; A. M. Potapov et al., 2022).

4.4. Acquisitive species are associated with higher basal fluxes

Consistent with our third hypothesis, faster growing species were associated with higher total fluxes. We found basal fluxes to be sensitive to litter phosphorus content, associated with higher litter decomposition fluxes, which is in line with the idea that high litter quality is more easily decompose (Freschet et al., 2012). Contrary to B. Wan et al. (2024), we did not find the litter C:N ratio to be a strong predictor of total energy fluxes, although it was included in one alternative model for SOM decomposition (Table S1.13).

Interestingly, legumes fuelled a higher rhizoflux, which was also reflected in total fluxes, highlighting the importance of this basal flux. Legumes have been identified as species able to produce P-mobilizing exudates (Wen et al., 2021), an ability that is associated with low morphological efficiency root systems (Wen et al., 2019), so opposed to the "do-it-yourself" strategy. Litter phosphorus content also positively affected rhizoflux, which includes fluxes from plants to their AMF symbionts, who play a key role in plant phosphorus acquisition (van der Heijden et al., 2015).

The ability to form nodules negatively affected bacterivory, which could be a consequence of its effect on *f:b* channel ratios for basal fluxes, as they support higher relative basal fluxes to fungi (higher $f{:}b_{\text{decomposition}}$ and $f{:}b_{\text{rhizoflux}}$). This is surprising, as legumes have been shown to promote bacterivorous nematodes (Kostenko et al., 2015; Ye et al., 2020), but it illustrates the quantitative and qualitative impact of the plant economic strategy on the soil food web.

On the other hand, contrary to our third hypothesis, the influence of AMF colonisation on fluxes to AMF was barely detectable. These results must be interpreted carefully, as their estimation presents methodological issues. The use of PLFA 16:1ω5 as an AMF-marker has been criticised, because of its

presence in some bacteria (Frostegård et al., 2011). It is indeed not realistic that the biomass of AM fungi would be almost equivalent in the presence and absence of plants: even if hyphae life-span can outlast its host (Pepe et al., 2018), they were most likely very disturbed when sieved during mesocosm preparation (de Vries et al., 2009), lowering their living biomass.

4.5. Limits and perspectives

A major strength of our study is the assessment of realistic trophic resource preferences of microbes using the ^{13}C PLFA signature based on isotope labelling and incorporation into microbial PLFAs and the ^{15}N signature of the microbial biomass, which allowed us to quantify the relative importance of litter and rhizodeposition. Our results highlight the importance of those parameters for modelling energy fluxes in soil food webs, in particular regarding the contribution of living-plant derived resources that are often ignored or only considered through herbivory. This is largely due to the consideration of microorganisms as basal resources for fungal and bacterial channels (Hedde et al., 2024; A. M. Potapov et al., 2019; B. Wan et al., 2022), while they are also primary consumers. Microbial contribution to the detrital channel is also consequential, as it represents more than 98% of the flux from 'brown' resources in our study and should be accounted for when trying to link soil food webs and ecosystem functioning.

Our study represents a first step towards quantitative estimation of microbial preferences for basal resources; however, further studies are needed to refine preferences estimation. Indeed, though preferences have little impact on total fluxes, they are important for assessing fluxes from different resources to microbes. Although our estimations are based on empirical data, they still have some limitations. In addition to the potential underestimation of litter decomposition in the plant+litter treatment, our model may also be biased due to our assumption that carbon use efficiency of both SOM and litter are similar, while there is evidence that carbon use efficiency also depends on substrate C:N ratio, nutrient limitation, and substrate oxidation state (L. Ma et al., 2024; Manzoni et al., 2010). Finally, the model has conceptual imperfections, especially concerning rhizodeposition. First, basal resources are not considered as finite pools which can be exhausted: their biomasses are only taken into account for weighting preferences. As such, this may not accurately reflect rhizosphere processes where multiple organisms compete for the resource they all prefer, up to its depletion (Garcia Arredondo et al., 2024). Moreover, our experiment does not allow for distinction between label obtained in the rhizosphere from the hyphosphere, and it has been shown that these different hotspots have specific microbial communities and different dynamics (Faghihinia et al., 2023).

The model we used is based on steady-state assumption (Jochum et al., 2021), which might be exaggerated for a mesocosm experiment with a duration of 3 months. However, a steady-state assumption is very common in functional ecology, for instance to determine litter decomposition rates (Cornwell & Weedon, 2014; Olson, 1963). Nonetheless, temporal variability may be a factor of particular interest for future

exploration, as there is evidence of a successional shift in microbial, nematode, and microarthropod communities during litter decomposition (Fujii & Takeda, 2012, 2017; Sauvadet et al., 2016).

Some of the conceptual issues we encountered are hot discussion topics. For example, the classification of rhizodeposits as detritus or as being part of a "green" channel is discussed in the recent 'Soil Food Web Ontology' proposed by Le Guillarme et al. (2023). Our results plead for their inclusion in the living-plant channel, in the same way nectar-feeding insects are considered herbivores and not detritivores, by highlighting different dynamics of litter decomposition and rhizoflux. Another discussion topic in the 'Soil Food Web Ontology' is the inclusion of an explicit internal vs. external digestion trait, which echoes our issue of quantification of the absorption efficiency for microbes. This illustrates the difficulty of having a conceptual framework including mechanisms relevant both for microbial and faunal processes, and underlines the need for further research.

5. Conclusions

By coupling a food web energetics approach with stable isotope probing in the microbial compartment, we have shown that rhizodeposition is an essential energy source for the soil food web with additive effects on basal fluxes that propagate to higher trophic levels, in particular to fungivorous springtails. On the other hand, fluxes from litter decomposition, while of the same order of magnitude as rhizoflux, seem to partially replace rather than supplement SOM decomposition. How plants influence belowground energetic pathways is also modulated by the economic strategies developed by plants to acquire their resources. This supports the idea of a strong functional interplay between plants, especially their rooting system and economic strategies, and soil organisms. We illustrate the utility of the food web energetics approach for studying ecosystem functioning and emphasize the need for more explicit inclusion of plant-derived basal resources by considering microbes as primary consumers and not only as the basal resources of fungal and bacterial channels.

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Chapter 3

Litter quality, plant growth, exploration strategy and bacterivory are determinant for litter-derived nitrogen recovery pattern in plant and microbial compartment for 13 grassland species

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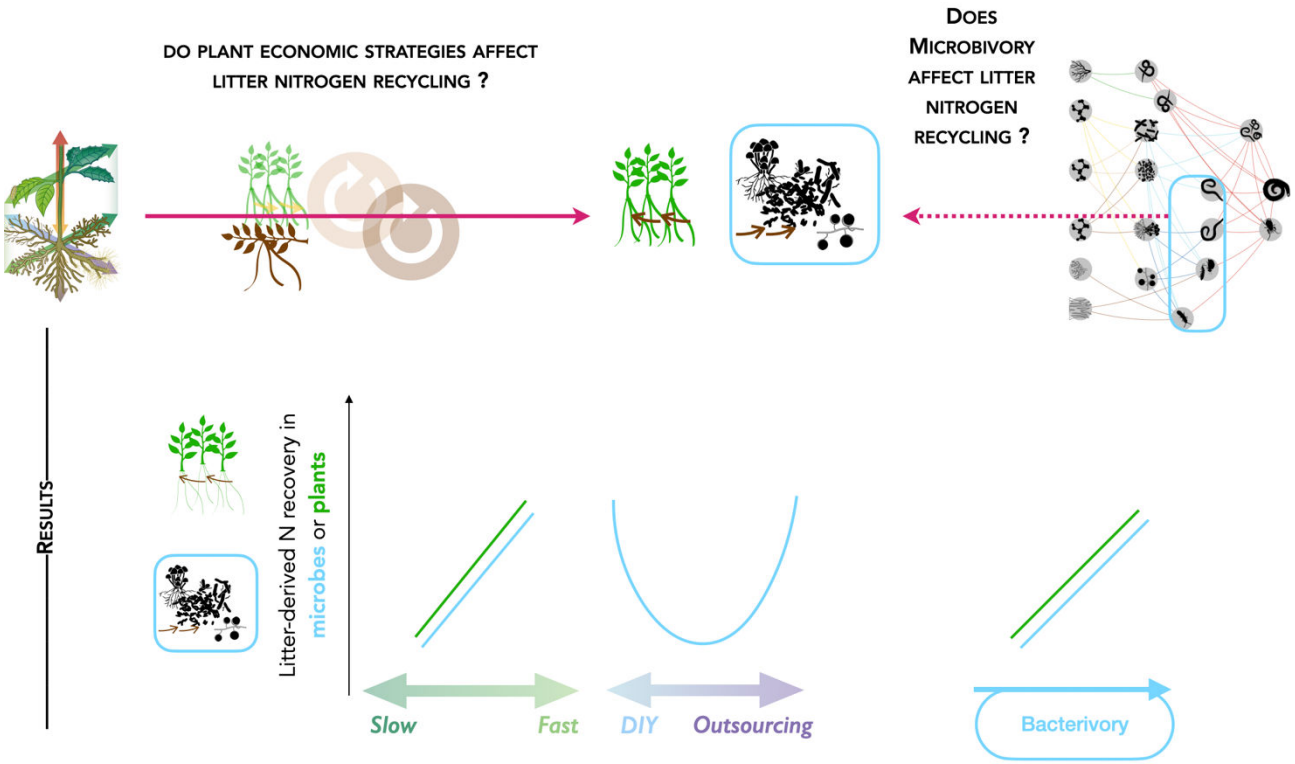


Abstract

Context. Litter properties conditioning decomposition are crucial determinants for long term ecosystem functioning, with acquisitive species better quality litter promoting faster decomposition rates. These "after life effects of plant economic strategy" are rarely considered together with living plant strategy, while living plant can strongly affect microbial decomposers by facilitation (with labile carbon inputs from rhizodeposits) and competition (through nitrogen (N) uptake), and thus, litter-derived nitrogen recycling. We do not know how belowground exploration strategy, opposing "do-it-yourself" species investing in morphologically efficient root systems to "outsourcing species" relying on mycorrhizal fungi for this function, despite evidence that even arbuscular mycorrhizal fungi lacking saprotrophic abilities can supply their host with litter-derived N. Microbivores also play an important role in releasing microbially immobilised N by grazing and excretion.

Methods and objectives. Using a common garden experiment with ^{15}N labelled litter of 13 grassland species, in presence or absence of living plants, we aim to evaluate how litter properties, plant economic strategies and microbivory fluxes affect litter recovery patterns in microbes, plant shoot, root system and soil organic matter.

Results. We found that plant presence strongly decreased litter-derived N recovery in microbial biomass, but that litter-derived N recovery was positively correlated to plant biomass recovery. Consistent with our expectations, high quality litter (low lignin, high phosphorus) induced higher recovery in the plant and microbial compartments, and faster growing species were associated with higher plant recovery. Contrary to our hypothesis, plant litter-derived N recovery was higher in "DIY" than "outsourcing" species, but it was equivalent in microbes, leading to a humped-shaped (quadratic) relationship between microbial recovery of litter-derived N and the exploration strategy. We also demonstrated the importance of bacterivory for litter-derived N recovery in shoot.

Discussion. Because most of our outsourcing species are legumes, who have access to another source of N via their symbiosis with N_2-fixing bacteria, it may not be possible to generalise this result to other acquisitive species.

1. Introduction

Nitrogen, a macro nutrient for all living organisms, is among the ones most commonly limiting plant growth. To cope with nitrogen limitation, but also with competition for other resources (light, water and space), different strategies of N-acquisition have evolved (Grime, 1977). Acquisitive species with fast growth take up large quantity of nutrients to fuel their biomass production (Reich, 2014). They tend to be rich in nitrogen, especially their leaves, as N is an essential component of enzymes required for photosynthesis: their short-live organs must be efficient to have a sufficient return on investment (Reich, 2014). On the other hand, conservative plant species adopt another strategy regarding N acquisition: they grow more slowly, but their organs have a longer lifespan, compensating for their lower efficiency, associated with higher dry matter content, and overall smaller N absorption rate.

Characteristics of plant's living organs predominantly determined properties of decaying organs (i.e., litter), influencing their decomposition rate. It is widely accepted that variation in litter properties along fertility gradients are part of a feedback loop reinforcing these fertility gradients (Hobbie, 1992). Yet, when considering not only leaf litter, but also root litter this relationship may be more complex (Hobbie, 2015). Investigating litter decomposability across plant organs, Freschet et al. (2012) demonstrated that litter with higher dry matter and lignin contents decomposed more slowly. If they did not find consistent relationships between litter nitrogen contents and decomposition rate across organs, other studies demonstrated that acquisitive species were associated with faster nitrogen cycling. This was true both for living plants (Henneron, Kardol, et al., 2020; Huang et al., 2021; Legay et al., 2016) and litter properties, including nitrogen content (Wambsganss et al., 2025), which promoted faster nitrogen mineralisation. Despite the importance of these mechanisms for plant soil feedback at the ecosystem scale, litter decomposition and living plant influence on nitrogen cycle are often studied separately. More studies are needed for understanding how whole-plant litter properties affect SOM decomposition and nitrogen mineralisation (both from SOM and from litter), in interaction with living plants. For example, new evidence demonstrates that roots reduced the quantity of litter-derived N but not C in SOM, suggesting that they promote litter-derived nitrogen decomposition selectively (Ridgeway et al., 2024).

Litter can be fragmented and incorporated in the particulate organic matter or end up in the dissolved pool, either directly for leachates or indirectly after depolymerisation for larger molecules. This dissolved N can then associate with minerals or be absorbed by microorganisms or plants (Wambsganss et al., 2025). Microorganisms can either immobilise dissolved nitrogen, or participate in net nitrogen mineralisation depending on stoichiometric conditions (Carrillo et al., 2017; Dijkstra et al., 2013): when carbon is in excess, all available nitrogen is used for growth, or for production of N-mining enzymes, while when carbon is limiting, excess nitrogen is excreted in mineral forms. This depends both on substrate C:N and microbial community stoichiometric constraints, as bacteria tend to have lower C:N ratio than fungi.

Microorganisms play a key role in litter nitrogen recycling, not only through their participation to mineralisation processes, but also because of their interactions with plants. These interactions can seem antagonistic at first glance, with the competition for nitrogen, but plant and microbes have different temporal niches for nitrogen absorption (Kuzyakov & Xu, 2013): upon arrival of the root in a soil volume, the high accessibility of readily available carbon from rhizodeposition promote strong microbial growth, leading to nitrogen depletion. This increases microbial nitrogen mining (Craine et al., 2007) and leads to higher total N availability for the plant after microbial biomass turnover, thereby resulting in mutualistic interactions. The release of nitrogen immobilised in the microbial biomass is essential for plant nutrition, and is greatly enhanced by the presence of microbivores, especially bacterivores (Trap et al., 2016). The latter have been shown to largely accelerate nitrogen mineralisation rate, both through direct excretion of mineral N, and through promotion of younger microbial cells with higher metabolic activity via grazing of senescent cells. They, too, are often overlooked in studies focusing on plant strategy effects on nitrogen cycle. Soil food web energetics, quantifying energy flows into soil food web, is a promising modelling approach to explore how soil fauna affect ecosystem functioning (Barnes et al., 2018), but it has not yet been applied to study how microbivory affect soil nitrogen recycling.

Other mutualists interactions related include symbiosis with mycorrhizal fungi and N_2-fixers bacteria. Arbuscular mycorrhizal fungi (AMF) are increasingly recognised as central players in the plant nitrogen nutrition, while their role was formerly thought to be centred on phosphorus acquisition, because of their limited saprotrophic abilities (van der Heijden et al., 2015). Indeed, AMF has been shown to colonise litter patches, enhancing plant N nutrition (Hodge et al., 2001; Hodge & Fitter, 2010).

AMF colonisation is determinant in plant acquisition strategy. Indeed, plant belowground economics strategies are increasingly recognised as multidimensional, with a trade-off reflecting soil exploration strategy by plants (Bergmann et al., 2020; Weigelt et al., 2021). The "outsourcing" plant species are associated to a large root diameter that can accommodate more mycorrhizal colonisation, while the "do-it-yourself" (DIY) species invest in their own root system for soil exploration, and have higher specific root length (SRL, unit length per unit root biomass). Thus, as both strategies (DIY vs outsourcing) allow for high soil volume exploration – when taking into account hyphal length (McCormack & Iversen, 2019) –, both strategies may lead to high litter-derived N recovery, independently of the acquisitive/conservative gradient.

Here, we aimed at exploring litter-derived N recovery patterns in plant and microbes across 13 grassland species with contrasting economics strategies, and how SOM cycling parameters and microbivory reflect this relationship. We hypothesized that plant economic strategies and litter properties are good predictors of litter-derived N recovery patterns, with acquisitive species featuring higher plant recovery, while conservative species promote higher microbial recovery of litter-derived N (H1a). We also hypothesized that both ends of the exploration gradient (do it yourself vs. outsourcing) are equally efficient in their

foraging strategies regarding N (i.e. we expected a humped-shaped relationship between N recovery by plants and the exploration gradient, H1b). We surmise that the influence of plant economic traits and litter properties on litter-derived N recovery patterns are mediated by changes in microbial biomass and associated functions such as CO_2 mineralisation (SOM respiration) and net nitrogen mineralisation (H2). Finally, we expect microbivory to enhance litter-derived N recovery in plants in comparison to litter-derived N recovery into microbial biomass (H3).

To test these hypotheses in presence and absence of living plants, we traced the fate of ^{15}N labelled litter N across different compartments: dissolved organic matter, microbial biomass, total SOM, as well as plant shoot and roots for 13 grassland species with contrasted strategies. We used microbivory, assessed from soil food web energetics calculations (Chapter 2), to explain ^{15}N recovery patterns, and plant strategies assessment from Chapter 1.

2. Materials and Methods

2.1. Experimental design

2.1.1 Set-up

Litter of 13 grassland plant species from three functional groups (legumes, graminoids, and forbs) were incubated for 3 months in an experimental garden, with or without the presence of living plants of the same species (7 individuals per pots). Species selection was based on trait values from the literature to cover the fast-slow trade-off within each functional group and the exploration trade-off overall (Table S1.1).

The pots were handled in three blocks, each containing one replicate of the 13, and 2 control pots with only soil. The 6-L pots (22 cm deep, 20.75 cm mean diameter) were filled at 0.8 $g \cdot cm^{-3}$ with soil collected in a permanent urban mesophilic grassland (0-20 cm depth) at 49°28'28.3"N 1°04'17.6"E in Mont Saint-Aignan (France) after 5 mm sieving, during which all visible macroinvertebrates were removed.

Litter of each species labelled with ^{15}N (10 atom%) was produced under hydroponic conditions (see Chapter 2, Supp. Mat. §1.2.1). In each pot, 0.7 g of root litter was incorporated into the first 7 cm, while 1.5 g shoot litter was deposed on the surface and sprinkled with the first soil centimetre to prevent wind scattering. Litter application amounts were calculated based on grassland plant productivity, detrital production, and biomass allocation from data available in the literature. To avoid biased litter availability compared to living plants, we also adjusted the amounts according to pot density (Supp. Mat. § 1.2.2).

Seedlings of each of the 13 species germinated until 2-leaves stage and then preserved at 4°C to synchronise the species before transplanting 7 individuals per pot on June 10th, 2022. Dead seedlings were replaced until the fifth week after transplantation. Plants were grown for three months in an outdoor experimental garden at 49°27'27.9"N 1°04'06.0"E, in Mont-Saint-Aignan (France). Soil moisture was kept above 60% of field capacity using automated watering, supplemented, if necessary, by weekly hand-watering based on pot weight.

2.2. Harvest and measures of variables of interest

2.2.1 ^{15}N Recovery

To estimate ^{15}N recovery, we determined the amount of ^{15}N in various compartments: total SOM, microbial biomass, dissolved organic nitrogen, belowground plant parts and aboveground plant parts by multiplying compartment size and compartment enrichment. ^{15}N recovery in microarthropods was not included in the total proportion recovered, as they represented less than 0.2% of inputs. All isotopic signature were measured with a Delta V Advantage Thermo Electron (Bremen, Germany) isotope ratio mass spectrometer (IRMS) and C content with a Euro EA 3000 EuroVector S.p. A (Milan, Italy) at the Centre for Stable Isotope Research and Analysis (University of Göttingen).

Pots were destructively sampled in September 2022. All aboveground plant parts were clipped 1 cm above ground, dried at 35°C for at least 48h, and powdered for isotope-ratio analysis. One complete undisturbed individual root system was sampled in each pot, and underwent the same treatment. Soil was sampled in three 0-7 cm deep, 5 cm diameter core, sieved at 2 mm and separated for further analysis in subsamples for microbial biomass estimation by fumigation-extraction, incubation for C and N mineralisation and isotope ratio analysis. Soil was dried at 35°C for 48h and powdered for isotope-ratio analysis. Soil microbial biomass was determined by the fumigation-extraction method according to ISO 14240 (1997) modified using an extractant concentration of 0.2 $mol \cdot L^{-1}$ K_2SO_4 solution to facilitate following isotopic measurement on lyophilised extracts (Makarov et al., 2015).

2.2.2 SOM cycling

Basal soil microbial respiration was assessed based on a 24h-incubation of 50 g (equivalent dry soil) at 23°C. Soil moisture was standardized at 60% ± 10% of water holding capacity before incubation. Produced CO_2 was measured with a Li380 CO_2 analyser on a subsample of the atmosphere of airtight pots filled with CO_2-free atmosphere After 5 days, extraction with 0.2 M K_2SO_4 was performed again to assess net mineralisation of soil organic N, calculated as the difference in extractable N content between the extraction after incubation compared to the unfumigated extraction used in microbial biomass determination.

2.2.3 Plant economic strategies

Subsamples of above- and belowground litter were analysed to characterise carbon quality (water-soluble compounds, cellulose, hemicellulose and lignin) by successive digestions with an Ankom Delta Fiber Analyzer and elemental contents (Mn, K, Mg, Ca, P) with an ICP spectrometer (iCAP 7000 Series, Thermo Fisher Scientific), except for C and N, assessed using an elemental analyser (Flash, 2000; Thermo Fisher Scientific, Cambridge UK).

In Chapter 1, we assessed plant economic strategies using morpho-chemical and physiological traits. We described a well-defined exploration gradient as the first axis of our exploratory PCA, which was moderately correlated with %AMF colonisation. We also demonstrated that in our experiment, morpho-chemical traits were bad proxies of the acquisitive/conservative gradient with sometime incoherent above/below ground pattern. These strategies were better reflected by the absolute growth rate (AGR) and gross rhizodeposition per gram soil (RhSoil). Thus, we decided for this chapter to concentrate ourselves on the first PCA axis and the %AMF colonisation to describe the exploration gradient, as well as AGR and gross rhizodeposition per gram soil to characterise the acquisitive/conservative strategies.

Briefly, AGR was calculated from total biomass divided by growth period (depending on block, 13 to 15 weeks). Rhizodeposition was assessed from ^{13}C recovery after pulse labelling during two consecutive days for 6 hours. Rhizodeposition was defined as the sum of soil K_2SO_4 extractable ^{13}C and $^{13}CO_2$ produced during a 24 h soil incubation. Positive score on PCA1 reflect high root diameter and high root cortex

fraction, while negative scores reflect high specific root length. Percentage AMF colonisation was measured based on ten observations of AMF presence across ten 1 cm fragments per species.

2.3. Statistical analyses

All analyses were conducted with R version 4.4.1. We removed extreme points (sensu 1st/3rd quartile +/– 3 times interquartile range) before statistical analyses to avoid skewing the mean compared to the median. These outliers, likely due to propagated measurement errors, accounted for a maximum of 3.9% of microbivory values and even less for other fluxes. We explored the effect of plant economic strategies, litter properties, microbial biomass and associated functions, and microbivory on litter-derived recover patterns for each compartment with separate linear mixed models (LMM) with the package lme4.

Three models were tested for each flux, except herbivory where we only tested (1) and (2):

$$\text{15N recovery} = \beta_0 + \beta_{Pl}Pl + \sum_{X_L}\beta_{X_L}X_L + b_B B + \epsilon \quad (1)$$

$$\text{15N recovery} = \beta_0 + \sum_{X_{Pl}}\beta_{X_{Pl}}X_{Pl} + b_B B + \epsilon \quad (2)$$

$$\text{15N recovery} = \beta_0 + \beta_{Pl}Pl + \sum_{X_\mu}\beta_{X_\mu}X_\mu + b_B B + \epsilon \quad (3)$$

$$\text{15N recovery} = \beta_0 + \beta_L L + \beta_{Bacterivory}Bacterivory + \beta_{Fungivory}Fungivory + b_B B + \epsilon \quad (4)$$

where ^{15}N recovery is the proportion of tracer recovered in a compartment, Pl is the presence/absence of plant, B is the block (random factor, 3 levels). X_L is a litter property amongst element content (Ca, K, Mn, P), and C:N ratio. X_{Pl} is a variable characterising plant strategy among AGR, PCA1 (exploration strategy score), PCA1^2, AMF colonisation and rhizodeposition. X_μ is a variable characterising microbial activity among microbial carbon (C micro), microbial C:N ratio, CO_2 mineralisation (Soil Resp.) and net N mineralisation. β are the fixed-effects coefficients, b_B are the coefficients for the block and species random-effects, respectively, and ϵ are the residuals errors. A model of the same structure as model (2) was also fitted to explain microbial activity variables.

Models were computed using the *lme4::lmer* function on data sets previously z-scored scaled, allowing to compute standardised regression coefficients that can easily be compared (β). To improve residuals normality, variables were transformed using ln(x+1) or logit(x) for percentages before scaling. Confidence intervals were computed with the *stats::confint* function.

For each model, we checked the importance of the random effect comparing the full model fitted with REML = T with a model without the random effect fitted with *nlme::gls* (method = "REML"), according to (Zuur et al., 2009). For the same set of explanatory variables, if the model without random effect was better for all compartments, it was removed.

For each model a selection based on the Akaike information criterion (AIC) was performed with the *MuMIn::dredge* function which tests all variable combinations. Models within two AIC-units of the best models were tested for collinearity between variables using the *car::vif* function, and those with variance

inflation factors > 5 were removed. For models with a structure based on (2), if rhizodeposition or AMF colonisation were not significant predictors, we refitted the models without theses variables, allowing us to include points for which values for these variables were missing.

When there was more than one model left (most of the time), we performed a model averaging with *MuMIn::model.avg*. For models with a random effect, marginal (R^2m) and conditional (R^2c) coefficients of determination for each model were calculated using the MuMIn package. R^2m is based on variance explained by fixed effect only, while R^2c is based on both fixed and random effects. Within the results section, means and 95% confidence interval are reported.

3. Results

3.1. General patterns of litter recovery

Overall, slightly more than 50% (56.4 ± 21.4%) of our ^{15}N label in both treatments (Pl+L and L) were recovered, mainly in soil organic matter, which contained more than 75% of recovered ^{15}N (Figure 1.A1). In absence of plants, ^{15}N recovery in the dissolved organic matter was almost 4 times higher than in the Pl+L treatment ($p < 0.001$), 10% higher in the microbial biomass ($p < 0.1$), and 7% higher in SOM ($p > 0.1$;Figure 1.A2). Enrichment of DN and microbial biomass nitrogen decreased significantly in presence of plants, by 30% (Wilcoxon paired-test, $p < 0.001$) and 20% (Wilcoxon paired-test, $p < 0.05$), respectively (Figure 1.B). Dissolved nitrogen compartment was also 70% smaller in presence of plants (Wilcoxon test, $p < 0.001$), which drives the difference of ^{15}N recovery in this compartment between treatments (Figure 1.C).

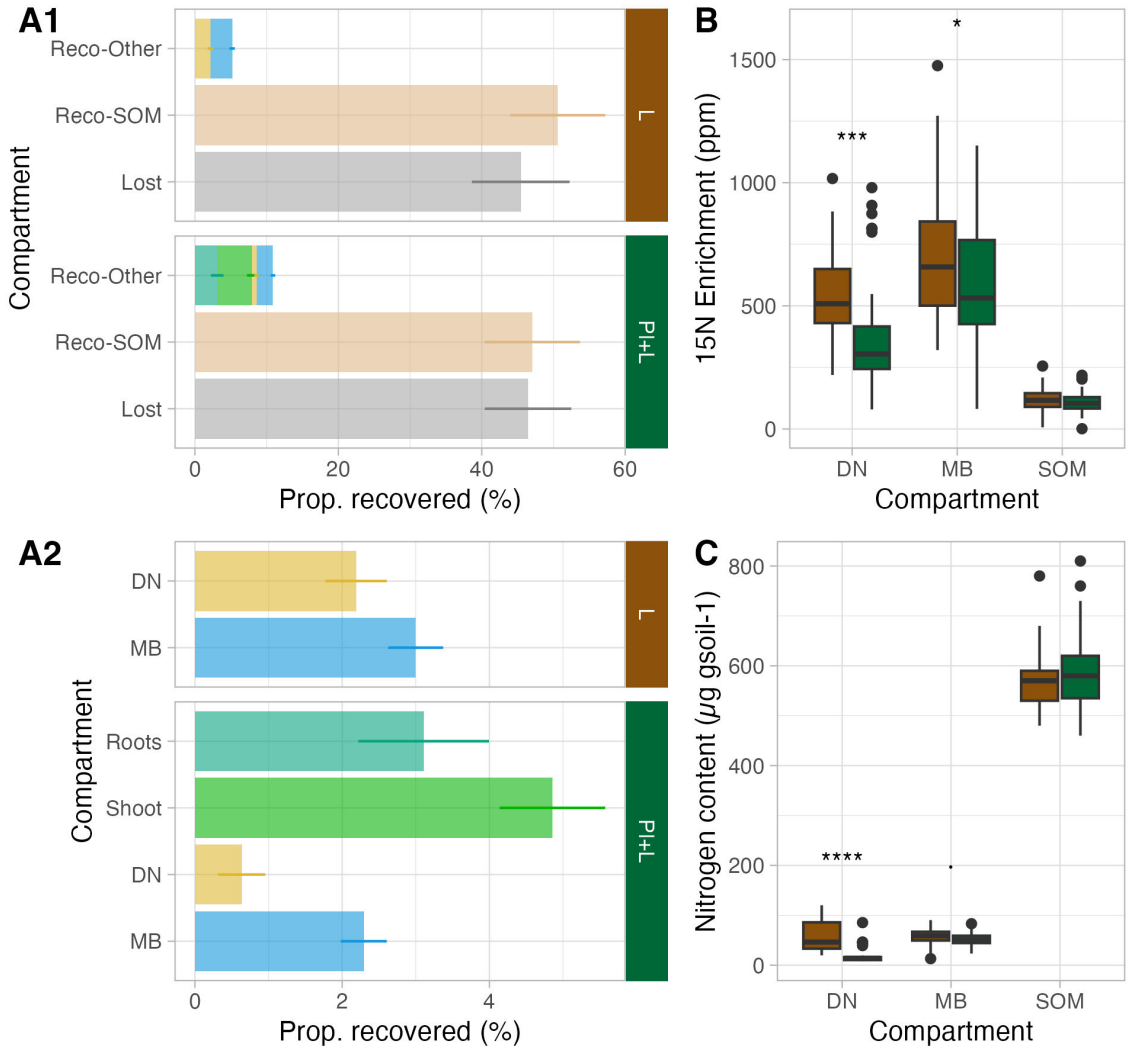


FIGURE 1 Patterns of litter-derived N recovery across compartments

DN: dissolved nitrogen, MB: microbial biomass, SOM: soil organic matter. Reco-Other: recovered ^{15}N in DN, MB, Shoot and Roots. Reco-SOM: recovered ^{15}N in SOM.

Proportion of litter-derived N recovery in microbial biomass explained 20% of plant N recovery ($p < 0.01$), with a positive relationship (Figure 2). Grasses showed higher litter-N recovery compared to other functional groups ($p < 0.5$, Wilcoxon's test), while there were no significant differences in litter-derived N recovery in microbes across functional group.

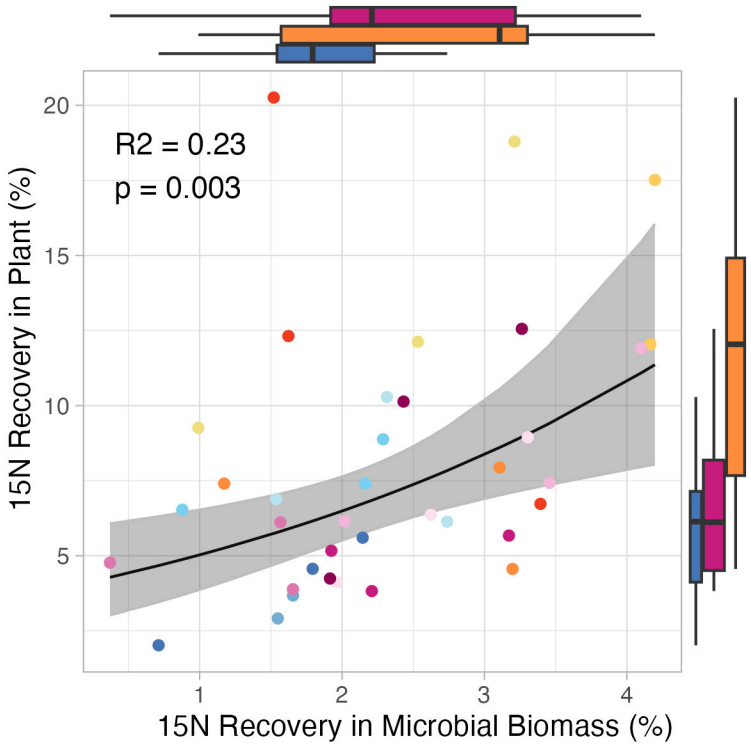


FIGURE 2 Relationship between Litter-derived N recovery in plant biomass vs microbial biomass

Linear regression on log transformed variables with 95% confindence interval, for the plant+litter treatment. Points are coloured by species. Side boxplots reflect functional groups (Blue: forbs, orange: grasses and pink: legumes).

On the other hand, legumes had higher total nitrogen that all other functional groups, and tended to have lower total microbial N in presence of living plant (Figure S1B).

3.2. Litter-derived N recovery patterns and economics strategies (H1)

Overall, plant strategies were relatively good predictors of ^{15}N recovery patterns in plant and microbial compartments, with either linear or hump-shaped relationships (Figure 3). Litter properties performed better than plant traits (Figure 4). Litter lignin content, particularly, was strongly negatively related to ^{15}N recovery in living compartments (β_{Lignin} = -0.25 ± 0.18, β_{Lignin} = -0.56 ± 0.08 and β_{Lignin} = -0.61 ± 0.14 for microbial biomass, above- and belowground plant biomass, respectively). Conversely, litter phosphorus content was associated with higher recovery in microbial biomass and in root systems (β_P = 0.62 ± 0.24 and β_P = 0.62 ± 0.35, respectively), while recovery in above ground plant biomass was positively affected by potassium (K) content and negatively by calcium (Ca) content (β_K = 0.47 ± 0.12 and β_{Ca} = -0.83 ± 0.18).

For living plant strategies, AGR was consistently positively associated with higher plant recovery (β_{AGR} = -0.50 ± 0.24 and β_{AGR} = -0.43 ± 0.28 for above- and belowground parts, respectively). Recovery was also associated with the exploration strategy, with a negative relationship between above ground plant

biomass recovery with PCA1 (β_{PCA1} = -0.49 ± 0.28) and a positive quadratic relationship between microbial biomass recovery and PCA1 (β_{PCA1^2} = 0.44 ± 0.32).

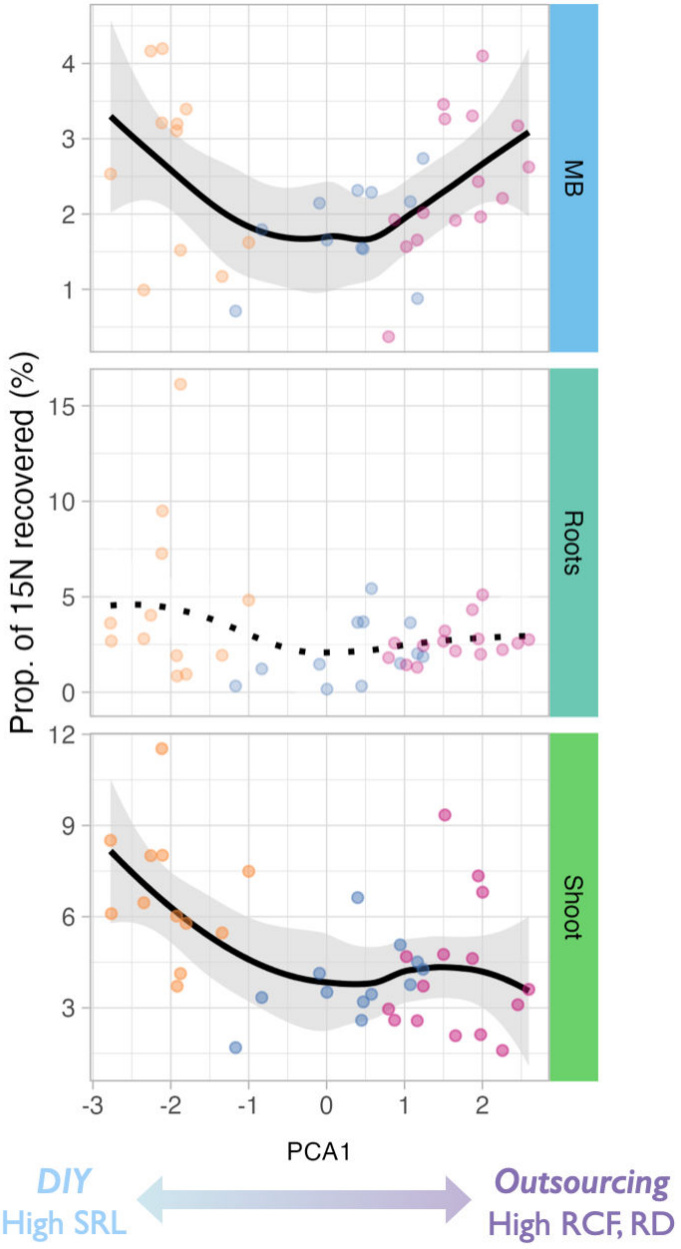


FIGURE 3 Univariate relationships between litter-derived N recovery in living compartments and the exploration gradient

The curve is a loess smoother to visualise the shape of the relationship. Smoother is dotted when the relationship is not significant in associated models (Fig.4).
Prop.: Proportion. MB: Microbial Biomass.

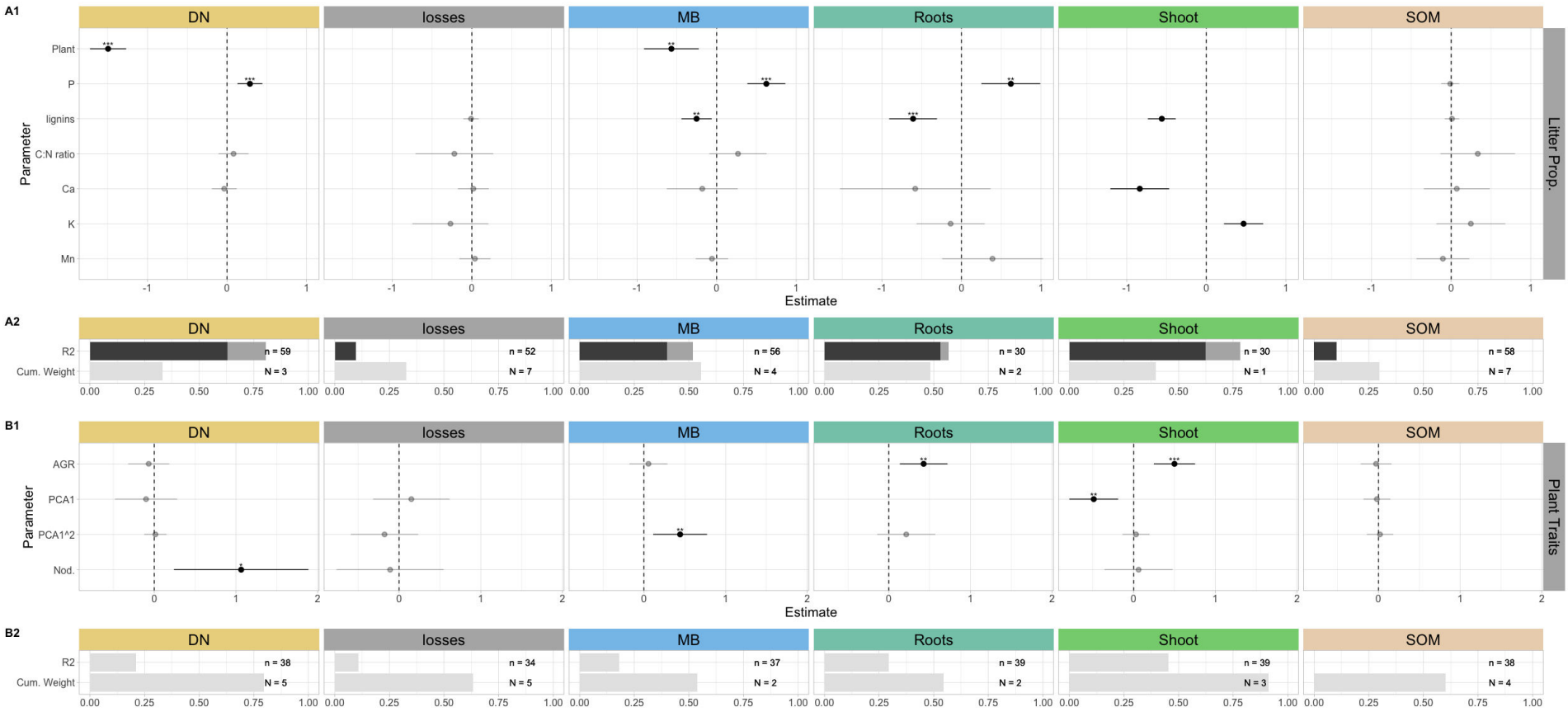
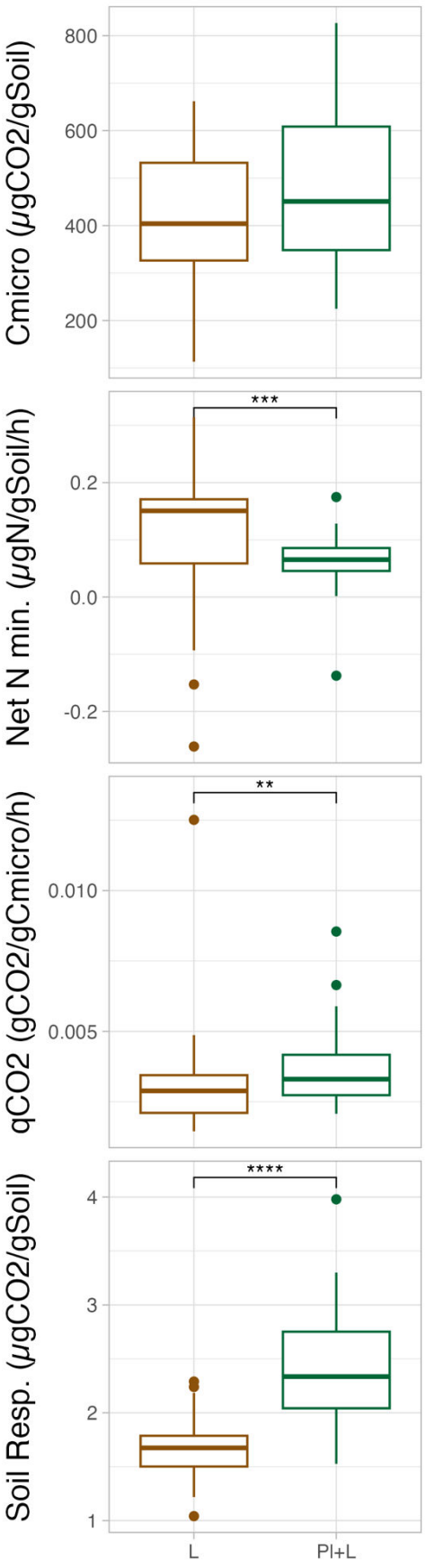


FIGURE 4 Parameters and properties of averaged models explaining proportion of ^{15}N recovery in various compartments by litter properties (A) and plant strategy (B)

Microbial biomass (MB); soil organic matter (SOM). Panels 1 present the (averaged) model coefficients with 95% confidence intervals (black indicates no intersection with 0). Panels 2 reports coefficients of determination R^2 of the best model (ΔAIC = 0), decomposed in marginal (dark grey) and conditional (grey) for models including a random effect, and sample size (n), as well as the cumulative AIC weights (Cum. Weight) of the N best models (ΔAIC < 2)

3.3. PES and microbial activity, microbial activity and recovery patterns (H2)



Plant presence affected most microbial parameters, to the exception of microbial biomass (Figure 5). Net nitrogen mineralisation decreased with plant addition ($p < 0.01$), while soil respiration, qCO_2 and *f:b* ratio increased ($p < 0.001$ and $p < 0.05$ respectively), compared to the litter-only treatment.

Overall, plant strategies were poor predictors of microbial activity (Figure S2), to the exception of rhizodeposition (expressed per gram soil), which had a strong positive influence on soil respiration and marginally on microbial metabolic quotient ($\beta_{RhSoil} = 0.43 \pm 0.29$ and $\beta_{RhSoil} = 0.18 \pm 0.33$). Litter phosphorus also positively affected soil respiration ($\beta_P = 0.32 \pm 0.25$).

Microbial activity were also relatively poor predictors of recovery patterns (Figure 6). Microbial C:N negatively affected microbial ^{15}N recovery ($\beta_{C:N\ micro} = -0.72 \pm 0.36$), while net mineralisation negatively affected DN recovery ($\beta_{N\ net\ min} = -0.32 \pm 0.16$) and positively SOM recovery ($\beta_{N\ net\ min} = 0.28 \pm 0.23$). Neither plant recovery nor losses were affected by microbial activity.

FIGURE 5 Variation of microbial activity across treatments

Soil Microbial Carbon Content (Cmicro), Net Nitrogen Mineralisation (Net N min.), Microbial quotient (qCO_2), Soil Respiration (Soil resp). C: control, L: litter-only, Pl: Plant-only, Pl+L: Plant+litter. Different letters indicate significant difference at 95% threshold (Wilcoxon test).

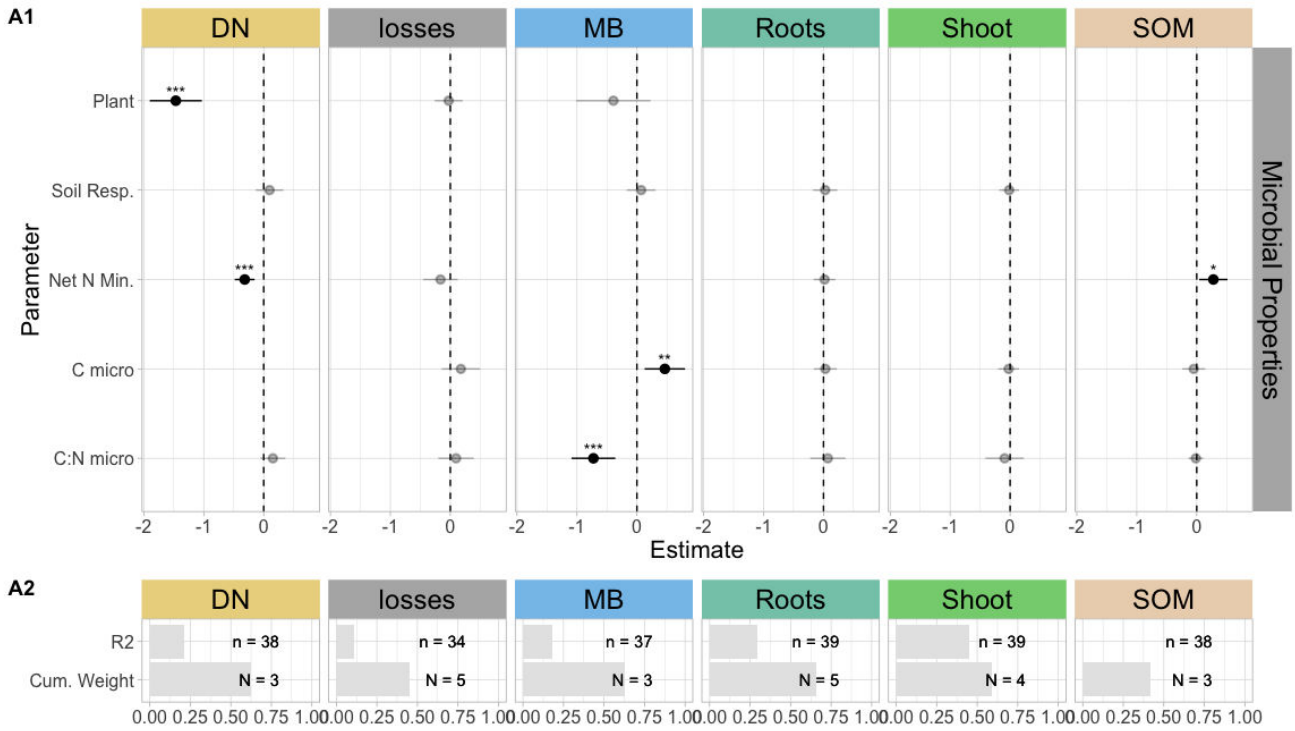


FIGURE 6 Parameters and properties of averaged models explaining proportion of ^{15}N recovery in various compartments by microbial activity and SOM cycling

Microbial biomass (MB); soil organic matter (SOM). Panel A1 present the (averaged) model coefficients with 95% confidence intervals (black indicates no intersection with 0). Panel A2 reports coefficients of determination R^2 of the best model (ΔAIC = 0, and sample size (n), as well as the cumulative AIC weights (Cum. Weight) of the N best models (ΔAIC < 2).

3.4. Microbivory and ^{15}N recovery patterns

Bacterivory was a strong predictor of litter-derived N recovery in above-ground plant biomass ($\beta_{Bacterivory} = 0.41 \pm 0.32$) and a moderate predictor of litter-derived N recovery in microbes ($\beta_{Bacterivory} = 0.33 \pm 0.23$), with higher bacterivory promoting higher recovery (Figure 7). Fungivory affected positively litter-derived N recovery in dissolved nitrogen ($\beta_{Fungivory} = 0.26 \pm 0.21$).

We also checked the correlations with the decomposition fluxes assessed by food web energetics (Figure S3), and found that it was significantly positively correlated with litter-derived N recovery in aboveground plant parts and microbial biomass. Litter decomposition flux was also positively correlated with bacterivory, and negatively with fungivory (Figure S3).

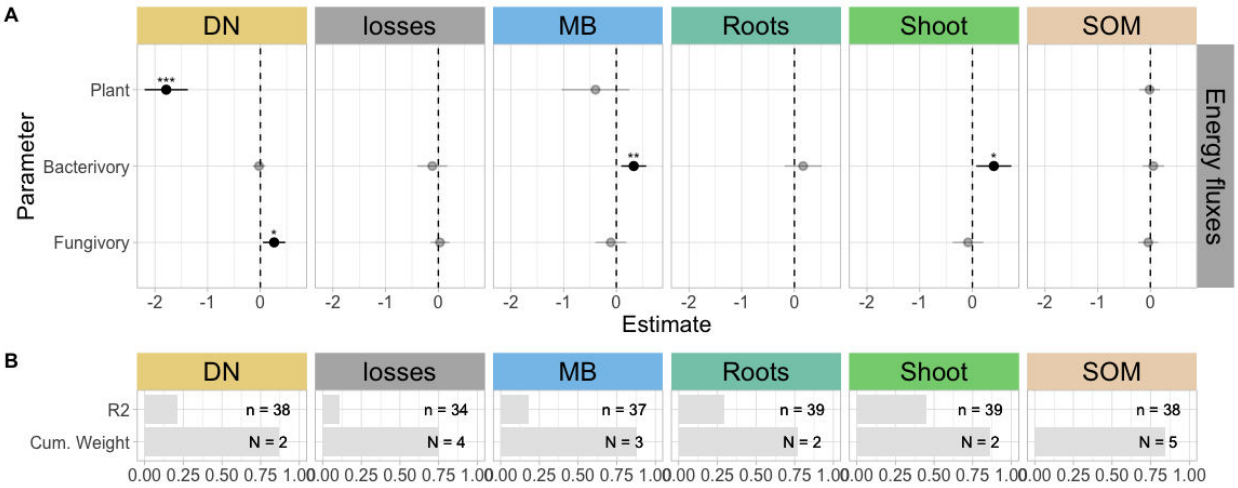


FIGURE 7 Parameters and properties of averaged models explaining proportion of ^{15}N recovery in various compartments by microbivory pressure assessed with soil food web energetics

Microbial biomass (MB), aboveground plant parts, belowground plant parts and soil organic matter (SOM). Panel A1 present the (averaged) model coefficients with 95% confidence intervals (black indicates no intersection with 0). Panel A2 reports coefficients of determination R^2 of the best model (ΔAIC = 0, and sample size (n), as well as the cumulative AIC weights (Cum. Weight) of the N best models (ΔAIC < 2).

4. Discussion

With this study, our goal was to identify the patterns explaining litter-derived N recovery patterns. In line with our first hypothesis, we demonstrated that plant economic strategies (especially litter lignin and P content, but also growth rate and exploration strategy) were moderately good predictors for litter-derived N recovery patterns in living compartments, that is, plant shoot and roots, as well as soil microbes (H1). However, we found little support for our second hypothesis, postulating that this influence would be mediated by microbial activity (H2). Indeed, microbial activity was barely affected by plant strategy (a little by rhizodeposition and litter P content), and it was a poor predictor of litter-derived N recovery patterns. Consistent with our third hypothesis, bacterivory was positively associated with higher N recovery within plants, endorsing the concept of the "microbial loop" (H3).

4.1. General patterns of microbial and plant recovery: between competition and mutualism

Microbial recovery of litter-derived N was negatively affected by plant presence (-10%), but at the same time was positively correlated with plant recovery. This may indicate some degree of competition between plant and microbes, which is supported by the large diminution of the dissolved nitrogen pool size (-70%), as well as the reduced net N mineralisation from SOM (-40%), in presence of plants.

On the other hand, plant presence also increased (+40%) microbially mediated carbon mineralisation from SOM, despite no difference in microbial biomass. Together with tracer dilution of the dissolved nitrogen pool (30% less enrichment in plant presence), this suggests "overflow" respiration due to N-limitation, accompanied by SOM-derived N mining, fuelled by rhizodeposition (Dijkstra et al., 2013; Mo et al., 2021; Schimel & Weintraub, 2003).

Surprisingly, total recovery did not differ between treatments, though we would have expected reduced losses in presence of plants. We can propose three explanations related to the experiment for this observation. First, the mass balance calculations for SOM, microbial biomass and dissolved nitrogen are based on the premise that soil volumetric mass has remained similar to that of the start of experiment in all pots, while it is probable that compaction occurred in all pots, leading to systematic underestimation of litter-derived N recovery in SOM and microbes, even more so in the treatment without plants, who likely suffered more compaction. Second, because pots were watered to maintain soil moisture over 60% of water hold capacity, higher evapotranspiration in treatment containing plants led to higher watering, thus potentially inducing higher leaching than in pots without plants. Lastly, due to a heat wave in August, pots were maintained at almost maximum water holding capacity to preserve the experiment, probably inducing leaching and creating temporary anoxic conditions favourable to high denitrification, thus homogenising losses across treatments. This episode may also have exerted a strong selective pressure on the microbial communities, which might also partly explain the similar microbial biomass across treatments.

4.2. Acquisitive and DIY species promote high plant recovery

We found plant economic strategies to be moderately good predictors for litter-derived N recovery patterns. More precisely, consistent with our first sub-assumption (H1a), we found that acquisitive species, with higher growth rate and litter of better quality (lower lignin and higher phosphorus content), absorbed more litter-derived N. However, the pattern was similar for litter-derived N recovery in microbial biomass, while we expected more microbial immobilisation in pots with conservative species. This suggests that, in our experiment, litter quality yield similar control on litter-derived N recovery in both plant and microbes, a conclusion further supported by the positive relationship between plant and microbial recovery. This is explained by the fact that, to the exception of soluble compounds like amino-acids, litter-derived N must be first processed by microbes (either intra- or extracellularly) in order to be absorbed by the plant. Thus, in our experiment, the most determinant factors for explaining patterns of litter N recovery were litter quality, which controlled the proportion of N that would become available for living organisms during the experiment through microbial decomposition, and plant absolute growth rate and specific root length, which determined the plant N uptake. Though we cannot ascertain whether this nitrogen has been absorbed directly by the plants (i.e., in competition with microbes) or after microbial turnover (i.e., temporal niche partitioning, as described by Kuzyakov & Xu, 2013), the strong relationship between litter derived recovery in above-ground plant parts and bacterivory (§4.4) supports the second explanation.

Coherent with our expectations, we also found the exploration gradient (based on a PCA axis opposing DIY strategy in negative values and outsourcing strategy in positive values) to have some predictive power for litter-derived N recovery patterns in plant and microbial biomasses. DIY species, in particular, showed strong litter-derived N recovery in shoots: their morphologically efficient root systems allow them to take up large quantities of nitrogen. However, contrary to our hypothesis (H1b), the relationship between litter-derived N recovery in plants was not quadratic but linear: outsourcing species did not recover as much as their DIY counterparts. We also detected a quadratic relationship with litter-derived N recovery in microbes. We acknowledge that, because most of our outsourcing species are legumes, there might be some confounding effect: this functional group can form symbiosis with N_2-fixing bacteria that supply with atmosphere-derived nitrogen for 20-80%[12] of their need (Peoples et al., 2015). As such, legumes are likely to rely less on litter-derived N for their nutrition than other functional groups, which may have led to the observed lower plant recovery. Nevertheless, their additional atmospheric-derived N supply could lead instead to luxury consumption and the higher total plant-N we observed, compensating for the lower relative importance of litter-derived N.

Further studies are needed to investigate how the exploration gradient and AMF colonisation affect litter-derived N recovery in living compartment, and SOM formation, particularly considering that the evidence

[12] These values correspond to the range of estimation across different species and with different methodologies presented by the authors, who aim at reviewing different methodologies measuring symbiotic N fixation in legumes. To our knowledge, there are no metanalyses on the subject.

of AMF influence on litter decomposition are contradictory (Wei et al., 2019): they might enhance the short term decomposition of fresh residues, while promoting the medium-term preservation of POM through protection in soil aggregates stabilised by the hyphal network.

4.3. Do microbes and associated functions mediate PES effect on recovery patterns?

Contrary to our second hypothesis, neither soil carbon and nitrogen mineralisation rates nor soil microbial biomass were obviously mediating plant strategy effect on litter-derived N recovery patterns in living compartments. Either litter represented a too small sub-pool compared to total SOM for its dynamic of decomposition to be reflected by the global respiration and mineralisation, or we measured parameters too coarse to reflect litter decomposition. Both explanations are not mutually exclusive. Indeed, soil respiration and net N mineralisation mix different sources: fresh litter addition, old detritus including fragmented grassland belowground litter (native particulate organic matter, POM) and native mineral-associated organic matter (MAOM). Not all pools are regulated by the same mechanisms: fresh litter addition and native POM decomposition will be mediated by depolymerisation enzymes, while MAOM decomposition will be controlled by desorption mechanisms (Daly et al., 2021; Ridgeway et al., 2024; Wambsganss et al., 2025). More, fresh litter will participate in the formation of new POM and new MAOM, thus further limiting the interpretation we can draw from our observations of litter-derived N in the SOM pool. It probably contains new POM and new MAOM, with both having different implications for the N mineralisation fluxes: new MAOM formation is possible only from solubilised litter-derived N, while new POM is undecomposed fresh litter. Gross N mineralisation may have provided more information, or better yet, N-depolymerisation enzymes activities, though both would still be subject to the "dilution" of fresh litter into native POM. Results on linkages between PES and N-cycle related enzymes are contrasted: Cheng et al. (2024) found higher N and C-cycling enzymatic activities under more acquisitive crop species, while Wan et al. (2022) found that C and P-cycling enzymes were associated with the fast/slow gradient, but not N-cycling enzymes. SOM rhizosphere priming and gross N mineralisation have been successfully associated with the fast/slow gradient (Henneron, Cros, et al., 2020; Henneron, Kardol, et al., 2020), showing that species with higher cycling rates also had higher N uptake.

Better consideration of the influence of litter-derived nitrogen dynamics is crucial not only for nitrogen cycle, with implications for plant nutrition, but also for carbon cycle, with implication for numerous soil functions, including structuration and climate mitigation. Indeed, it has been shown that molecules with a lower C:N ratio were more likely to be involved in organo-mineral association (Jilling et al., 2018; Kopittke et al., 2020), so considering litter-derived C and N together could advance our understanding of SOM formation.

4.4. Bacterivores participate in a "microbial loop"

Coherent with our third hypothesis, we found that bacterivory enhanced plant recovery of litter-derived N, though only in the above-ground parts. This result may also participate in explaining the plant strategy effect on litter-derived recovery patterns, as we demonstrated in Chapter 2 that the presence of nodules was associated with lower bacterivory. Interestingly, higher bacterivory was also associated with higher litter-derived N recovery in microbes, which suggests that bacterivorous nematodes either promote higher microbial turnover (Trap et al., 2016) or higher litter decomposition (which has been demonstrated in freshwater ecosystems, though not systematically; De Mesel et al., 2003; Ribblett et al., 2005). In our case, bacterivory was strongly correlated with litter decomposition ($R = 0.47$, $p < 0.001$, data not shown), as well as SOM decomposition. This supports the "microbial loop" concept (Bonkowski, 2004; Trap et al., 2016), predominantly based on bacterivores, as we did not find any effect of fungivory on litter-derived N recovery in microbial or plant compartments. However, we did find that higher fungivory (but not bacterivory) was associated with higher ^{15}N recovery in the dissolved organic pool, which is complementary with de Vries et al. (2013) finding that springtails were associated with increased dissolved organic carbon leaching in European soils. Their limited impact on other compartment relative to bacterivores may be explained by the fact that the bacterivorous nematodes have C:N ratio 50% higher than their preys, while springtails' C:N ratio is three times lower (A. M. Potapov et al., 2022), leading to much higher mineralisation rates of bacterivores. Slower turnover of fungal biomass may also affect litter-derived N recycling.

5. Conclusions

With this experiment, we demonstrated that N litter recycling to the benefit of plant and microbes depends of plant strategy, both on the fast/slow gradient with litter structural (lignin content) and chemical (P content) properties along with growth rate, but also on the exploration dimension, with "DIY" species morphologically efficient system allowing them to recapture more litter-derived N. We highlighted the need for more investigation on the "outsourcing" end of this gradient, to evaluate whether the lower recovery is inherent to this strategy, or if it is here confounded with legumes' symbiont ability to fix atmospheric nitrogen.

We did not find evidence microbial biomass nor mineralisation processes to explain the PES influence on litter-derived recovery patterns, but further investigation of more precise mechanisms such as priming, gross nitrogen mineralisation or enzymatic activities might provide more insights. Finally, we demonstrated the importance of bacterivores in nitrogen cycling, contributing to the argument of their explicit inclusion in models.

6. Acknowledgments

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General discussion

1. Preamble: results synthesis

The aim of this PhD was to explore how rhizodeposition and litter inputs influence plant and soil biota, and how these effects are modulated by plant economic strategies. In the following paragraphs, we summarise the answers to the three questions that structured this manuscript.

HOW DOES RHIZODEPOSITION FIT IN THE PLANT ECONOMICS SPACE, AND HOW DOES THIS SHAPE THE MICROBIAL COMMUNITY?

In the first chapter, we measured a wide range of morpho-chemical but also physiological leaf and root traits, and followed the fate of carbon from recent photosynthates with PLFAs stable isotope probing in 15 grassland species, with or without litter addition.

We demonstrated that, in line with our hypotheses (H1.1), belowground physiological traits fitted logically in the plant economics space: higher root respiration for acquisitive species, higher degree of mycorrhizal colonisation for outsourcing species, and higher rhizodeposition for legumes, who are both acquisitive and outsourcing. Yet, we did not find the expected relationships between absolute growth rate and traits widely used to characterise the fast/slow gradient. Traits also showed different response to litter addition, both in direction and intensity, not always coordinated within a strategy – e.g. both root dry matter content and absolute growth rate were positively affected by litter addition. This outlines some limits of the plant economics space framework, that will be developed in §2.1.

We found that all microbial groups were dependant on recent photosynthates, and that, contrary to our expectations (H1.2), biomass and ^{13}C enrichment were differently affected by plant economic strategies. Zygomycota's relative biomass was the only one affected by rhizodeposition, but their enrichment was not (while all other groups' enrichment were). AMF biomass was positively associated with the degree of root colonisation, but also surprisingly with the "DIY" strategy, while its ^{13}C enrichment was related to specific root respiration. This highlights the need for more explicit investigation of biotic interaction in the PES (§2.2), notably by better understanding the multiple facets of rhizodeposition (§2.3).

WHAT IS THE RELATIVE IMPORTANCE OF LITTER AND RHIZODEPOSITION FOR SOIL FOOD WEBS?

In the second chapter, we used a $^{13}C/^{15}N$ dual labelling approach coupled to soil food web energetics to quantify the relative importance of litter and rhizodeposition as basal resources for soil food webs.

By integrating explicitly these two resources in the soil food web for the first time, rather than considering bacterial and fungal biomass as basal compartments as it is commonly done, we demonstrated, in line with our expectations (H2.1), that despite different pool size, litter and rhizodeposition fuelled energy channels of comparable size. In partial support of our hypothesis 2.2, we found that decomposition fluxes shifted from fungal dominance to bacterial dominance with plant addition, but fluxes from rhizodeposition largely

supported the fungal channel, up to fungivorous springtails. This underlines how intricated the resource channels and spatial compartments approaches are (§2.4, §2.5).

Finally, we also demonstrated that plant strategies affected energy fluxes, with higher litter phosphorus content promoting higher basal fluxes from litter and rhizodeposition, while species with higher growth rate were associated with higher total fluxes (H2.3).

HOW DO PLANT ECONOMIC STRATEGIES AFFECT LITTER NITROGEN RECYCLING?

In the last chapter, we looked at the distribution of litter-derived nitrogen in various compartments. We found that litter-derived N recovery in microbes was strongly reduced in presence of plants, but that microbes and plant recovery were correlated. This is explained by the fact that, in partial support of our first hypothesis (H3.1), we found that high litter quality (low lignin and high phosphorus content) was determinant for high recovery in both plant and microbial compartments. Higher plant growth was also associated with higher litter-derived recovery in shoot and root systems. This has determinant consequences for ecosystem functioning (§2.6).

Contrary to our second hypothesis (H3.2), we did not find our coarse indicators of microbial activity (namely microbial biomass, net N mineralisation and microbial respiration) to reflect those changes, suggesting that our indicators were not specific enough to decomposition processes to detect changes across our modalities.

In line, with our third hypothesis (H3.3), we demonstrated that even though bacterivory was unaffected by plant strategy (Chapter 2), it was a strong predictor for litter-derived N recovery pattern in plant and microbial compartments, highlighting the importance of stoichiometric differences between trophic levels for nitrogen cycling (§2.4.2).

2. Discussion and perspectives

2.1. The root economics space: limits, extension and perspectives

The root economics space is a relatively recent concept (Bergmann et al., 2020; Weigelt et al., 2021). Matthus et al. (2025) reviewed the fresh evidence (posterior to Bergmann et al., 2020) concerning this theoretical framework. Their meta-analysis (Figure 1) found strong empirical support for a belowground multidimensional trait space (demonstrated in more than 80% of the review literature), including the exploration gradient (demonstrated in around 80% of the reviewed literature) and the fast/slow gradient (confirmed in around 70% of the review literature), and their orthogonality (supported in around 50% of reviewed literature). Our results fit relatively well in this conceptual framework, as we clearly identified the exploration gradient, while the fast/slow gradient was less evident (Chapter 1).

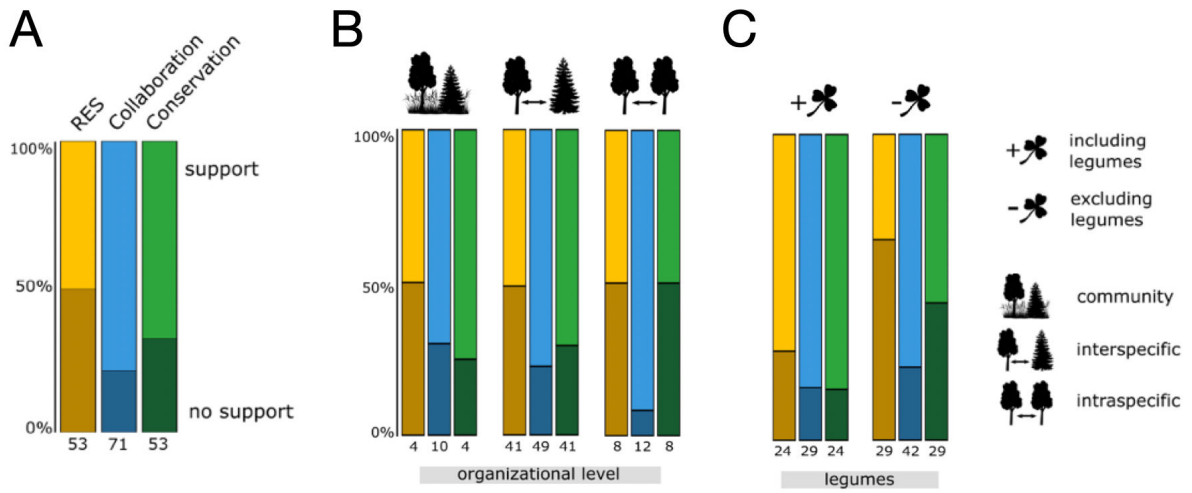

FIGURE 1 The concept of the root economics space and its support in the literature (Matthus et al.,2025)

Proportion of studies supporting the root economics space (RES) concept (yellow), defined as the presence and orthogonality of both collaboration [exploration] gradient (blue, characterised by the negative correlation between root diameter and SRL) and the conservation [fast/slow] gradient (green, defined by the negative correlation between root tissue density and root nitrogen) for A) the whole data set, B) split across organizational level and C) the presence of legumes (Fabaceae) *in the species set. Light shade indicates support while dark shade indicates no support. B.*

The power of this concept is the simplicity of trait measured and its robustness across scales, but it has the weaknesses of its strength: integrating more traits, particularly physiological traits, are necessary to advance towards a better understanding of belowground plant functioning.

This concept also has limits: in this section, we will discuss in more detail how the interaction between phylogenetic constraints and intraspecific variability (§0), the multifunctionality of traits (§2.1.2), and how implicit integration of biotic interaction restricts interpretation, notably across the examples of mycorrhization and nodules (§2.2).

2.1.1 Intraspecific variation and phylogenetic constraints

Intraspecific variation, i.e., the phenotypic trait variation within a species, is determined by "genetic differences among populations, plastic responses to environmental gradients and ontogenic changes" (Laughlin et al., 2017). This variability can be described by the ***magnitude*** and the ***direction*** of trait variation across environment. It is often considered negligeable compared to interspecific variability, and thus species mean are often used in trait-based ecology, a practice which is increasingly challenged (Albert et al., 2010; Siebenkäs et al., 2015). Notably, for aboveground traits, intraspecific variability can represent up to 30% (Siefert et al., 2015).

Magnitude of trait response to environmental conditions is species dependant, thus leading to inconsistent "strategy-ranking" of species across different environments (Figure 2; Albert et al., 2010; Craine, 2009; Siebenkäs et al., 2015). This can lead to apparently incoherent findings, with conservative species rich in nitrogen in rich soils (Chapter 1) and acquisitive species with high C:N ratios (Cardenas et al., 2021).

Direction of trait response to environmental conditions is trait-dependant. Divergent response of traits

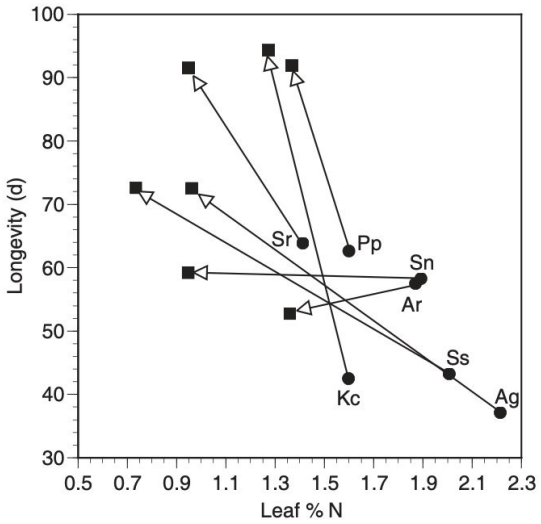

FIGURE 2 Relationship between leaf longevity and leaf nitrogen concentration for 7 grassland species across two experiments with soil of contrasted nitrogen contents (Craine, 2007)

Arrows connect points from the same species in the higher (circles) and low (squares) soil nitrogen content.

supposedly coordinated can lead to weakened interspecific relationships (Figure 3). Laughlin et al. (2017) demonstrated this weaking in field measurements compared to experimental conditions, but despite our controlled experiment, this may have been what we observed in our Chapter 1, when litter addition increased both AGR and RDMC, while we expect these two traits to be negatively related.

The topic of intraspecific variability is gaining a renewed interest in trait-based ecology (Chacón-Labella et al., 2023). While most studies on intraspecific variability are centred on above-ground traits, belowground traits, caught between the necessity of high plasticity for water and nutrient foraging and strong phylogenetic constrained on morphological traits, are particularly worth investigating.

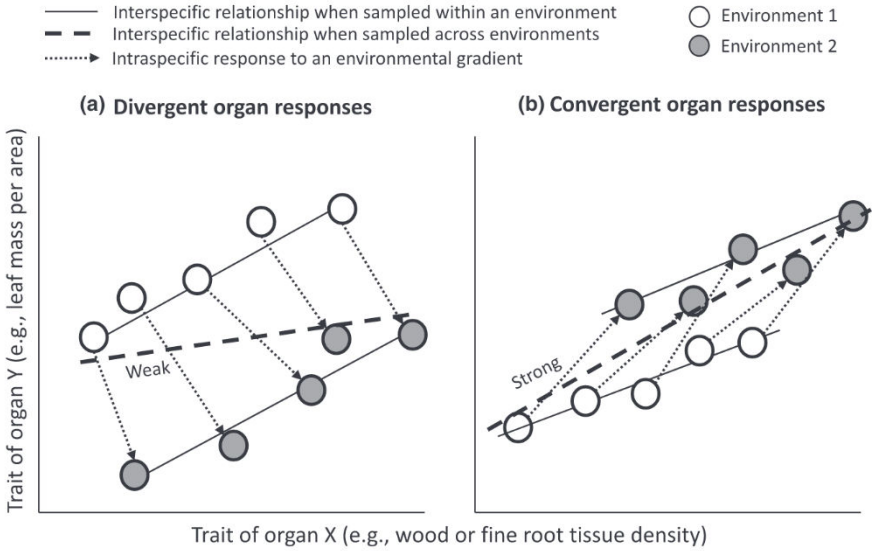

FIGURE 3 Theoretical representation of decoupling in the interspecific whole plant economics spectrum due to divergent organ responses (Laughlin et al., 2017)

Root plasticity is a clear advantage for the optimisation of foraging efficiency despite high spatial and temporal variability in nutrient bioavailability. Morphological and architectural[13] plasticity in response to nutrient patches is well documented (Mou et al., 2013), coupled with understanding of hormonal pathways driving the regulation of root plasticity (Jia et al., 2022). Interestingly, this response includes control of root hair formation and density, but root hairs are often overlooked in the plant economics space framework.

Though a large part of intraspecific variation is explained at the local spatial scale (Weemstra et al., 2021), family can explain more than 50% of variance of root morphological traits, across woody and non-woody species (R. Wang et al., 2018). The different magnitude of phylogenetic signal across traits can blur the orthogonality of both RES axis: RNC and RMD display the strongest phylogenetic signal[14] (Valverde-Barrantes et al., 2017), but they are related to supposedly independent gradient (see Box "The Special Case of Legumes"). Phylogenetic constraint can also have considerable repercussion on above-/belowground linkages: while the phenotypic response of herbaceous species to low light is an increase in SLA at constant shoot mass fraction, increased root mass fraction contributed 2.5 times more to the total root length increase in response to low nutrient than SRL changes (Freschet et al., 2015). Phylogenetic constraints are increasingly accounted for in studies, by presenting two sets of models, including or not a correction for the phylogeny (Laughlin et al., 2017).

[13] Architectural traits are traits determining the "spatial configuration of the root system as a whole" (Bardgett et al., 2014). They include for example rooting depth, or branching intensity.
[14] Though it is weaker in non-woody species (Kong et al., 2019).

> IN A NUTSHELL, root traits are highly plastic both across environment and at local scales to adapt to soil resource heterogeneity, but at the same time, some are strongly conserved across phylogenetic families. This may impede the detection of trait coordination.

2.1.2 Root trait – function linkages are complicated

Poorter & Ryser, (2015) suggested that trait multifunctionality could explain the contrast between high chemical, morphological and architectural plasticity at very local scale and strong conservation of morphological root traits.

> *"An important contrast between leaves and roots is that the latter are not 'simply' the terminal parts attached to stems and branches and their task is not only to take up nutrients and water. The root system is a continuously expanding organ. Moreover, it also has to provide anchorage and transport, which requires a certain amount of support and transport tissue." (Poorter & Ryser, 2015)*

Freschet et al. (2021) illustrate this concept of how a trait may be related to multiple functions with the example of root nitrogen content. If the importance of RNC for ecosystem N cycling is demonstrated, including ***plant acquisition***, the assumption that it is a good proxy for root metabolic activity – mirroring the strong relationship between LNC and photosynthetic rates – may be premature. Though it is a relatively good proxy for root respiration, it may not be extendable to specific root uptake activities. Indeed, root N may also result on trade-off related to other functions, like nitrogen ***storage*** (see below, non-reproductive belowground organs) or ***defence*** (see §2.2), as chemical defensive molecules are often rich in nitrogen.

The multifunctionality of plant traits is a limit of the plant economics space framework, centred around plant resource acquisition. Other frameworks, such as the "global spectrum of plant form and function (GSPFF)" (Díaz et al., 2016) also include stem and seeds related organs, and when extended to root economics traits, they do not find above-belowground coordination (Carmona et al., 2021), rather that the root economics space captures additional variation, leading to heated debate (Bueno et al., 2023; Weigelt et al., 2023). One argument was that, in the GSPFF × RES framework of Carmona et al., seed traits had no analogous component belowground, leading to an unbalanced comparison between above- and belowground plants parts. Yet, a wide range of non-absorptive belowground organ can be involved in reproduction, especially among grassland species (Klimešová et al., 2018). The growth form determined by these non-reproductive organs have been show to affect "economic" root traits, with for example stoloniferous clonal species [15] displaying higher SRL, lower RTD, and lower %AMF colonisation (Klimešová & Herben, 2021), and could be an interesting addition to the global spectrum of plant form and function. Moreover, integrating non-acquisitive belowground organs in the PES would be an essential addition to use this framework for understanding plant communities' assemblage. For example, compared to Grime CSR theory, fast growing species in the PES encompass both fast growth as a competitive advantage in rich and stable environments (competitive strategy), but also in disturbed environment where

[15] In our study, *Trifolium repens* a stoloniferous clonal species, indeed has one of the highest shoot:root ratio of all our studies, and one of highest SRL compared to other legume species.

a species must quickly resolve its life cycle (ruderal strategy). These theoretical considerations can have concrete applications: for example understanding how stress and disturbance affect plant communities of estuarian wetlands is essential for informed management decisions in light of the global changes that will affect these ecosystems (Neupert et al., 2025).

> IN A NUTSHELL, beyond the PES centred around nutrient acquisition, root systems are involved in a wide range of functions spanning from anchorage and stress resistance to vegetative reproduction, which are essential for plant community assemblage. It is important to acknowledge that some traits included in the PES can participate to several functions, and thus, that the traits we measure may result from other trade-offs that we did not study.

On the other hand, functions also result from multiple traits, which are not necessarily independent of each other. Freschet et al. (2021) term traits that result from interactions between other traits "composite traits".

For example, SRL is approximately a mathematical function of root tissue density and root mean diameter, according to the formula (Ostonen et al., 2007).

$$SRL = \frac{4}{\pi \times RMD^2 \times RTD}$$

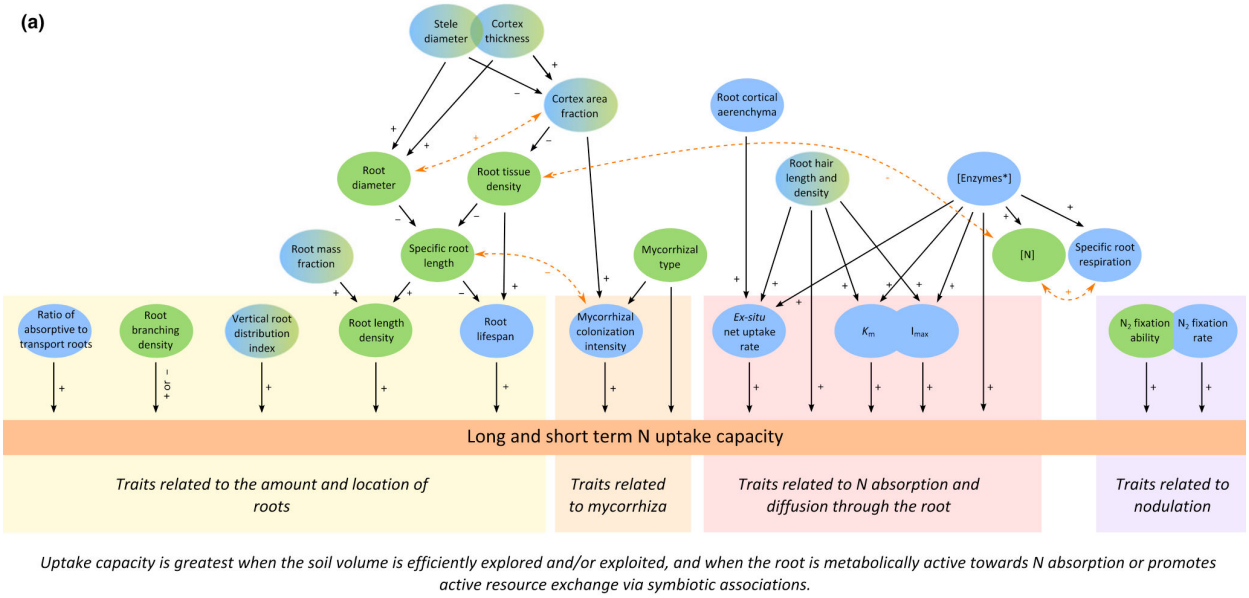

FIGURE 4 Direct, indirect and hierarchical relationships between the root traits related to long- and short-term nitrogen uptake (Freschet et al., 2021)

Vertical axis depicts hierarchical relationship, with upper levels representing "underlying" traits, black arrows indicate positive (+) or negative (-) relationships. Emergent covariations are shown in orange dotted arrows. "Hard" and "Soft" traits are shown in blue and green, respectively. This classification is based on the ease of trait measurement. I_{max} is root maximum net ion-uptake rate and K_m is root Michaelis-Menten constant.

This was an argument for the unidimensional root economics spectrum, opposing acquisitive species with high SRL to conservative species with high RMD and high RTD. However, RMD and RTD are not independent from each other: because root cortex thickness tends to increase faster than stele radius with root diameter (root allometry), and both tissues do not have the same properties (stele is enriched in structural content and depleted in nitrogen compare to root cortex), leading to a negative correlation between these traits, and thus dominance of RMD in predicting SRL. The emergent relationships related to root cylinder shape and root allometry have been proposed as core factors explaining root traits bi-dimensionality (Y. Zhang et al., 2024).

Disentangling the underlying relationships between traits is important to evaluate whether coordinated traits have been selected for individually or interdependently (Craine, 2009), and better identify the link between individual traits and functions. For example, nitrogen uptake is determined by quantity of roots and explored volume, activity of root (metabolic efficiency), as well as symbiosis (Figure 4), and the core root traits of the root economics space (SRL, RMD, RTD/RDMC and RNC) are only components of determinants of nitrogen acquisition.

In this study, we considered that all root traits below 2 mm were fine absorptive roots (Figure 5a). In order to better focus on nutrient acquisition, one can distinguish absorptive roots from transport roots (Figure 5b), based on root order or morphology (Freschet, Pagès, et al., 2021; Freschet, Roumet, et al., 2021; Laliberté, 2017; McCormack et al., 2015). Grasses, in particular, may have transport roots of less than 2 mm.

> IN A NUTSHELL, because root traits are not independent from each other, it is essential to understand the underlying determinant of composite root traits, and to acknowledge that no function is determined by a single trait. Some functions, especially nutrient acquisition, are also the result of biotic interactions.

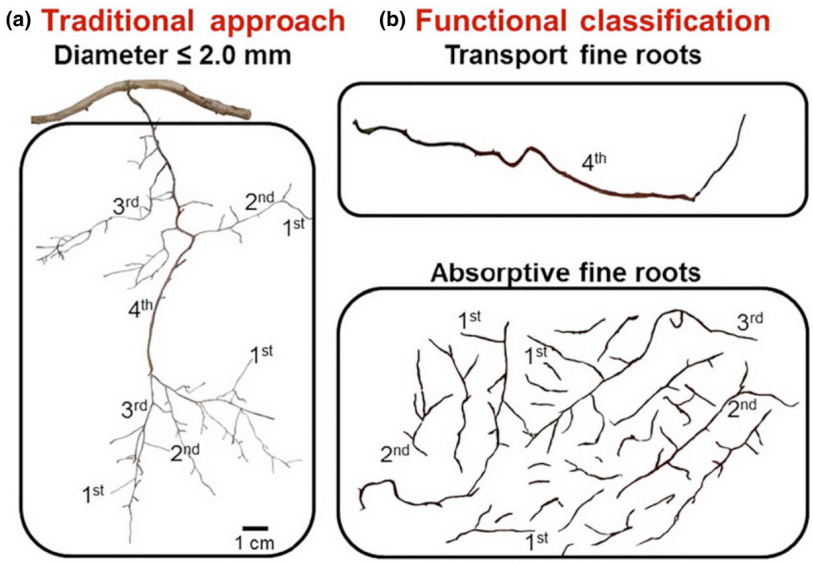

FIGURE 5 Representation of fine roots classifications (McCormack et al., 2015)

2.2. The need for more explicit integration of biotic interactions in the PES

Soil microbes are essential for SOM cycling and nitrogen mineralisation in particular. Pathogens also play a crucial role in plant performance. Yet, soil microbes are barely considered in the plant economics space, to the exception of mycorrhizal fungi, who characterise the outsourcing strategy of the exploration gradient. Regardless, they are not always explicitly considered, and when they are, it is rare that this consideration extends beyond mycorrhizal type and proportion of root length colonised.

2.2.1 Better characterisation of the exploration gradient

In 2017, Etienne Laliberté included integrating mycorrhiza in his six "belowground frontiers in trait-based plant ecology". If progresses have been made with the identification of the exploration gradient, which begins to answer his question "do mycorrhizas represent independent dimensions of plant below-ground functional variation?", there is still much to unravel.

Even within arbuscular mycorrhizal fungi (Class: Glomeromycetes), who are much less diverse than ectomycorrhizal fungi (Subkingdom: Dikarya, Divisions: Ascomycota, Basidiomycota), large variation in traits like degree of root colonisation, external hyphal length, phosphorus uptake or foraging precision have been demonstrated (Šmilauer, Šmilauerová, et al., 2020; Van Der Heijden & Scheublin, 2007). These traits are but examples of how AMF traits may be functionally relevant for the PES. In this manuscript, we contributed to the exploration of this "frontier" by quantifying not only degree of root colonisation, but also allocation of recent photosynthates to mycorrhizal fungi (approximated by the enrichment in the 16:1ω5 PLFA). Our findings emphasize the need for better understanding of the symbiosis, as the degree of root colonisation was not a good predictor for AMF enrichment. Perhaps the number of arbuscules, the exchange organ between plant and fungi, would have been a better indicator than degree of root colonisation. Perhaps the allocation to AMF at the time of labelling does not reflect the dynamic leading to the establishment of the mycorrhiza during the whole growth period. Other studies investigating the relative abundance and richness of AMF taxa compare to other fungal functional guilds failed to demonstrate higher AMF abundance/richness in outsourcing species, despite higher degree of root colonisation, both in monospecific conditions and in communities of variable species richness (Hennecke et al., 2023, 2025). These elements give a small overview of just *how much* there is this to unravel on this thematic.

The "do-it-yourself" strategy would also benefit from better characterisation. As we saw in the previous section of this discussion, SRL alone is a limited predictor of soil volume exploration, and should be completed be root mass fraction, root length density (length root per soil volume) and/or architectural traits like root branching intensity. This would not only better inform this dimension of root strategy, but also help for strategy/function linkages, as exploration of root volume is likely to be determinant in competitive plant/plant interactions.

> IN A NUTSHELL, the exploration gradient should be evaluated with traits integrating more explicit measurement of soil volume exploration, including traits of external hyphae, and characterisation of plant/AMF interaction, beside the simple degree of root colonisation. This would help to characterise biotic interaction, not only plant/mycorrhizal fungi symbiosis but also plant/plant competition.

2.2.2 Beyond mycorrhization: other biotic interactions in the PES

Mycorrhizal fungi are not the only microbes to interact with plants. As we demonstrated in Chapter 1, all microbial groups were significantly labelled after 2 days of pulse labelling. Among them are probably mutualist decomposers and plant-growth promoting bacteria, opportunists and pathogens.

Plant economic strategy have been shown to influence fungal community in mixed plots (Hennecke et al., 2025): plant pathogen were more abundant under acquisitive and DIY species – highlighting once more multifunctionality (mycorrhization probably participates to plant defence), though the same pattern was not found in monocultures (Hennecke et al., 2023).

The same studies did not find effect on the abundance of saprotrophs, but they highlighted shifts in saprotroph community along the fast/slow gradient, suggesting adaptation to high litter production of better quality or lower organ turnover with more recalcitrant properties for acquisitive vs. conservative species, respectively.

With our PLFA-based classification, we could not distinguish root pathogens from saprotrophs, but it is likely that at least some of the enrichment we found in the saprotrophic fungi comes from pathogenic taxa. Another group that may participate to the enrichment of non-mycorrhizal fungi is the dark septate endophytes (paraphyletic Ascomycota[16]). They are facultative plant symbionts with saprotrophic capacity whose effect on plant growth are context dependant, but they can substantially enhance plant absorption of macro and micronutrients from organic material (Vergara et al., 2017). Transfer of carbon and nutrients from the plant have been demonstrate but it is unclear whether they take place within our outside the root (Ruotsalainen et al., 2022). Though they might participate in trade-off relative to the exploration gradient, they have not, to our knowledge, been investigated in the light of the plant economics space. Because they occurred in our experiment, we measured their degree of root colonisation along with AMF's and did not find any significant correlation between degree of colonisation by dark septate endophytes and the other traits we measure in our experiment (data not shown).

[16] Because we don't have the isotopic signature of 18:2ω6,9 due too low detection by the GC-IRMS, this limit does not apply to our study.

Box 1: A specificity of legumes?

Legumes (Family: *Fabaceae*) can participate in symbiosis with N_2 fixing bacteria like *Rhizobia* (Phylum: alpha-proteobacteria) or *Frankia* (Phylum: actinobacteria). This could represent an alternative strategy for nitrogen acquisition, independent of the exploration gradient. However, in our case legumes tended to have the highest root diameter and cortex fraction, and functional group was almost confounded with the exploration gradient, because this gradient in strongly constrained by phylogeny.

Using a phylogenetically informed principal component analysis on a larger dataset, Weigelt et al. (2021) found the species participating in symbiosis with N-fixing organisms to be aggregated at the acquisitive side of the fast/slow gradient but also to span a wide range of values along the exploration gradient (Figure 6).

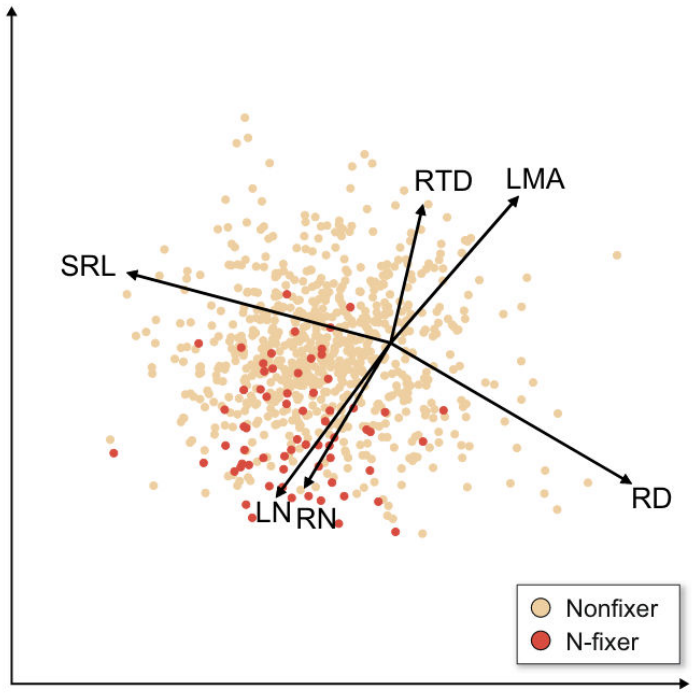

FIGURE 6 Phylogenetically informed principal component analysis based on species' mean value trait for 804 species (Weigelt et al., 2021)

PCA axes represent 30.1% (x) and 27.5% (y) of variation.

Better explicit consideration of legumes' specificities in PES studies may be essential for advancing our understanding of biotic interactions in the PES. Phylogenetically-informed statistics are one way to do that (Marcellus et al., 2024), but investigating it would also be interesting to test legume's intraspecific trait variability to nodulation inhibition (using mutant or high N-soils, for example). Integrating non legume species that occupies similar functional niche may be another way to do that.

Like with AMF, only reporting the symbiosis possibility may be insufficient: characterising whether the symbiosis is realised is crucial, but methodologies to do that are still complex (Peoples et al., 2015). Some functional traits like nodules shape (Chmelíková & Hejcman, 2012) or biomass (Dayoub et al., 2017) may provide insightful data. Other traits of interest for this symibiosis include for example root phosphatase activity (Marcellus et al., 2024): less constrained by N-limitation than other plants, legumes invest more in phosphate solubilisation. AMF also playing a key role in phosphate acquisition (van der Heijden et al., 2015), this may explain why, without phylogenetic correction, legumes species tend to cluster on the outsourcing end of the gradient (Chapter s1, Matthus et al., 2025).

Evidence on the relationship between PES and bacterial communities are still scarce, as the few studies investigating microbial communities tend to focus on fungi. In a bioRχiv preprint, Wu et al. (2023) found that the PES across 52 tree species had little influence on bacterial communities, who were more impacted by soil parameters like pH. On the other hand, studying intraspecific variation of *Pinus massoniana* across

22 sites, Lin et al. (2024) found that copio- and oligotrophic bacteria were associated with the acquisitive and conservative strategy, respectively.

> IN A NUTSHELL, as formulated by Matthus et al. (2025) "*the variety of mechanisms behind root trait-microbe relationships (root chemistry and decomposition, exudation, priming effects, litter quantity etc.), and strong expected dependencies on environmental conditions might make it difficult to detect generalizable patterns but the literature on this is still scarce*".

2.3. Towards better positioning of rhizodeposition in the plant economics space

Rhizodeposition quantity and quality is at the intersection of plant/soil/microbes interactions. Some studies have focused on plant exudation rates and composition (Cheng et al., 2024; Sun et al., 2021; Williams et al., 2022) while other consider rhizodeposition as a whole and rhizosphere priming effect (Guyonnet, Guillemet, et al., 2018; Henneron, Cros, et al., 2020; H. Wang et al., 2025). In both cases, while the association of higher rhizodeposition/exudation with acquisitive attributes is relatively clear, there is mixed evidence for the relationship with the exploration gradient (Matthus et al., 2025). Our results blend right in this ambiguous evidence, with legumes' ability to form nodules being the predominant factor in our models, and inconsistent effects of the exploration dimension depending on whether we look at models results or overall correlations (Chapter 1).

Wen et al. (2021) argue that root exudation should be integrated explicitly as a component of belowground strategy: an alternative to the binary trade-off between morphological/architectural efficiency and mycorrhizal symbioses (Figure 7). They further emphasize the need for better classification of root exudates in functional categories (in his framework P-mining carboxylates, and N-priming exudates). For them, exudates also fall along a "do-it-yourself" vs "outsourcing" gradient, as P-mobilizing exudates have a direct effect on physico-chemical process while N-priming exudates.

There is definitely a pattern in the composition of root exudates across strategies and functional groups, but so far, the interpretation is largely limited by low identification of the molecules, which impairs mechanistic understanding (Williams et al., 2022).

Once again, multifunctionality must be accounted for: indeed, root exudation patterns are the results of interactions between many processes including molecular signalling pathways, defence and allelopathic compounds, or losses due to concentration gradients, beside those previously mentioned. Thus, exudation patterns varies not only across species but also between environments (Dietz et al., 2020), and with the addition of soil fauna (Levasseur et al., 2025).

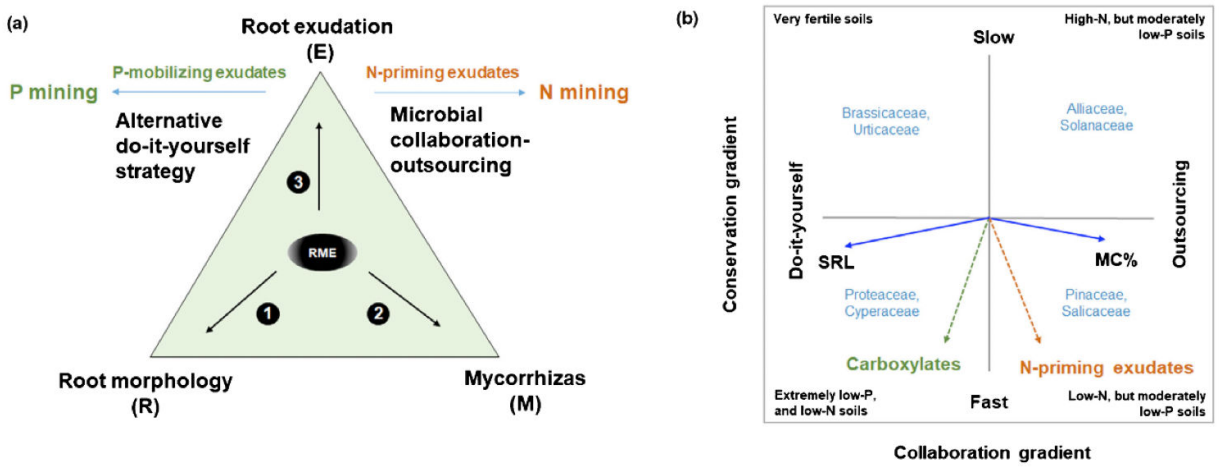

FIGURE 7 Conceptual framework linking root exudation to belowground economic traits in resource acquisition (Wen et al., 2021)

Please note that slow growing species being associated with very fertile or high N moderately low P soils is somewhat contradictory with other frameworks linking PES and ecosystem functioning (see General Introduction)

Notably, most methods for measurement of root exudates implies collection in water, which limits our understandings of the impact of biotic interactions, though progresses have been made with studies on plants grown in the field and transferred in water only for exudate collection (Oburger & Jones, 2018). These "rhizosphere solution" are usually filtered before analysing, removing slough of cells, which may lead to underestimation of rhizodeposition when focusing on root exudates (Dennis et al., 2010). The predominant role in structuration of rhizosphere bacteria communities compared to other rhizodeposits carbon pools has been questioned (Dennis et al., 2010): largely concentrated at the root apex (see Figure 15, General Introduction), exudates are unlikely to be the principal determinant for root bacteria community away from the apex, where lysate from senescent cells or root hairs turnover dominate rhizodeposits.

Methods of rhizodeposits collection in soils and in relatively undisturbed rhizoboxes (Figure 8) are a promising approach to gain a better knowledge of rhizodeposition as a whole (Levasseur et al., 2025). They allow for chemical characterisation without focalising on root exudates. Because they are non-destructive and specifically localised, they provide a great opportunity for quantitive and qualitative exploration of rhizodeposition spatio-temporal patterns (Garcia Arredondo et al., 2024). This is one of the next "frontiers" in the understanding of rhizodeposition, maybe with the characterisation of "hyphodeposition", that is molecules derived from recent photosynthates (Faghihinia et al., 2023; Kaiser et al., 2015).

Description of how root exudation and rhizodeposition as a whole varies across soil types, nutrient patches or along the root will greatly advance our understanding of rhizosphere processes and belowground plant economic strategies.



FIGURE 8 Arrangement of the nitrocellulose traps on the roots of *Linum usitatissimum* in the rhizoboxes, the glass window removed for the rhizobox was placed on the left (credits: Estelle Forey)

Temporal fluctuation of rhizodeposition rate have also been gaining interests, with for example characterisation of multiple rhizosphere parameter (pH, Eh, O_2, dissolved organic carbon) across day/night cycles (Garcia Arredondo et al., 2023), emphasising the importance of mineral-organic interactions for short-term (day) regulation of dissolved organic carbon availability for microbes. At a larger timescale (year), rhizodeposition is also seasonal, with probable impacts on microbial communities and higher trophic levels that depend on this resource.

> IN A NUTSHELL, description of root exudate and/or rhizodeposits composition is but at the beginning, and the path is long before the whole range of their functionalities is elucidated but it may be a necessary step to integrate them fully in the plant economics space, as different strategies may be associated with certain groups of molecules. Resolving spatiotemporal dynamics of rhizodeposition is one of the challenges ahead, and may help in characterising rhizodeposits functions.

2.4. Integrating *f:b* channels with spatial compartmentation

2.4.1 Explicitly considering microbes as consumers: challenges and perspectives

In other studies using soil food web energetics modelling (Hedde et al., 2024; A. M. Potapov et al., 2019; B. Wan et al., 2022), rhizodeposition is often overlooked as a basal resource, using directly bacteria and fungi as the base of their respective energy channels, while litter is only integrated as a food for detritivores (mostly macrofauna). We clearly highlighted the necessity of considering microbes as primary consumers of these resources: in order to correctly integrate the spatial compartment approach with the bacterial vs fungal channel approach, we need to acknowledge the dependence of both these microbial groups to recent photosynthates. We also shed light on the difficulties associated with this approach, notably assessing realistic trophic preferences for microbial groups, and considering microbes' external digestion.

We will discuss here the first one in more details. A dual $^{13}C/^{15}N$ labelling allowed us to estimate empirically the consumption of recent photosynthates by different microbial groups, and litter consumption as a whole, thus providing a novel estimation of the relative importance of both resources for soil food webs. Considering the rate of soil biodiversity loss, and the detrimental consequences that subsequent functional losses would have on ecosystem services, a fine resolution of trophic links and preferences – including rhizodeposits – are essential for future monitoring of soil health/quality.

Though this was a first step in the right direction, a design allowing for comparable estimation of both rhizodeposition and litter within microbial groups, either with a $^{13}C/^{14}C$ dual labelling or supplementary treatments with unlabelled plants and ^{13}C labelled litters would greatly facilitate the estimation of microbial groups' preference of rhizodeposition and litter. This would also avoid the problem of underestimation of litter decomposition fluxes in presence of plant due to their N-uptake (see Box 2).

Box 2: Contradictions between Chapter 2 and 3?

While estimating indirectly litter decomposition with different methods in Chapter 2 and 3, we arrived at contradicting conclusions. In Chapter 2, we found an apparent partial substitution of SOM decomposition fluxes by litter decomposition fluxes, suggesting negative priming, but in Chapter 3, lower enrichment (i.e. ^{15}N dilution) of the dissolved N pool in presence of pool rather implies positive priming (additional SOM-derived N mining).

Because the latter is a direct measurement and does not involve multiple hypotheses for its calculation, we suggest taking with caution this particular result from Chapter 2: there may be additivity between fresh litter and native SOM decomposition fluxes, even though we did not detect it, because of the underestimation of litter-decomposition flux in presence of plant

2.4.2 Separated microbial groups and stoichiometry: a promising approach for modelling mineralisation fluxes in soil food webs…

However, simultaneous characterisation of C and N dynamics would also yield interesting results, especially considering the role that difference in stoichiometry between resource and consumers plays in organic matter decomposition dynamics (Buchkowski et al., 2019), both at the microbes (Mooshammer et al., 2014) and microbivores levels (Trap et al., 2016).The regaining interest in stoichiometry is notably visible by the recent publication of a large stoichiometric database of organisms across biomes and ecosystems (González et al., 2025).

The *soilfoodwebs* R package provides methods to integrate stoichiometry in soil food web modelling by modulating organisms' diet and carbon use efficiency to fit their demand (Buchkowski et al., 2023; Buchkowski & Lindo, 2021). Integrating stoichiometry in soil food webs modelling is particularly interesting when investigation food web influence on mineralisation processes (Chapter 3), which was one of the main goals of the first soil food webs modelling (Hunt et al., 1987).

This package also provides ways to estimate the response to change (dynamic and not equilibrium-based estimation), and some sensitivity analyses functions. Sensitivity analyses are essential to better identify the

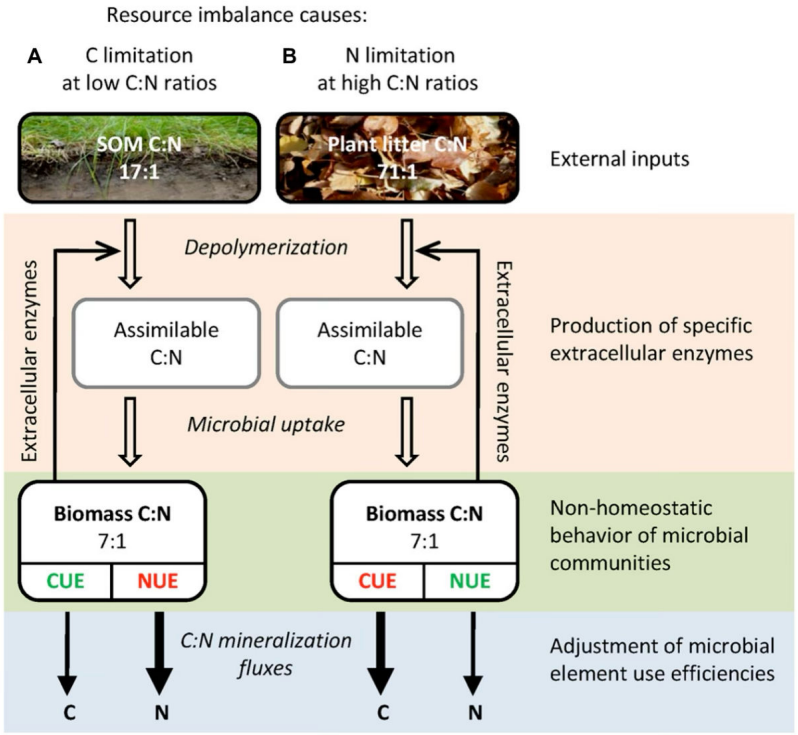

FIGURE 9 Simplified schematic representation of important C:N component and fluxes during organic matter break down by soil and litter microbial communities (Mooshammer et al., 2014)

limits of the models and direct the efforts, depending on the research issue. For example, we found[17] that small changes in microbial groups preference barely affected total fluxes, while they had strong influence in the estimation of the relative importance of litter and rhizodeposition for soil food webs.

Testing our more detail approach of the microbial compartment coupled with stoichiometry in natural or managed ecosystems would be essential for validating our conclusions. At a larger scale, taking into account seasonal variations in resource availability and associated shifts in microbial communities may also provide deeper insights in ecosystem functioning in relation to soil food webs (Birgander & Olsson, 2021).

2.5. Green, brown, fungal, bacterial, root-derived, detritus… Which channels are we keeping?

If Buchkowski et al. (2019, 2023) also plead for the explicit inclusion of elemental limitations of both animals and microbes, considering the latter not as basal nodes but as consumers of the detritus pool, their model omits one plant-based resource: rhizodeposition, which has a different C:N ratio compared to the detritus pool. This leads to consideration of a "green" channel including only herbivores, while we plead for the inclusion of rhizodeposits in a living plant-derived channel (Le Guillarme et al., 2023). Rhizodeposition is essential in order to take AMF into account. Our results emphasise their importance up to fungivorous springtails level, contrasting with the finding that microarthropods predominantly feed

[17] Though we did not do a formal sensitivity analysis: these observations were made during the fine tuning of microbial preferences, during which we tested different sets of preferences to find something that fitted our data.

on saprotrophic fungi (Pollierer & Scheu, 2021). This discrepancy may be explained by functional differences between arbuscular and ectomycorrhizal fungi, who may be less palatable due to higher defence compounds concentration (Freschet, Roumet, et al., 2021). We also clearly demonstrated different dynamics of saprotrophic vs. arbuscular mycorrhizal fungi, which resonate with discussion on the pertinence of including AMF in *f:b* ratios as ecosystem functioning (Norris et al., 2023; Strickland & Rousk, 2010). Diving deeper in the question of microbial trophic position with amino-acid finger printing, Steffan et al. (2015) argued that microbes, similar to animals, encompass different trophic levels, from herbivorous-like fungi to some kind of apex predators bacteria. This emphasises the importance of better assessment of microbial preferences in soil food web modelling, as heterogeneous nodes have been demonstrated to be major source of uncertainty (Buchkowski & Lindo, 2021).

Macro-detritivores were not included in our study, so an estimation of green and brown channels including both herbivores, microbes depending on rhizodeposits and/or detritus but also macro-detritivores as consumers of basal resources would greatly advance our understanding of soil food web partitioning. Protists are also often overlooked in soil food webs modelling, while, as bacterivores, they are essential for remobilising nitrogen immobilised in microbial biomass (Geisen, 2016; Trap et al., 2016).

> IN A NUTSHELL, considering microbes as consumers in soil food webs modelling is a hot topic, essential for reducing uncertainty in soil food web modelling, but also for compartmentalisation issues. Indeed, the fungal vs. bacterial channels are not as clearly separated when rhizodeposition is accounted for, and rhizoflux may considerably change how we perceive the relative importance of the "green", living plant-derived channel compared to the "brown" detritus-based channel.
> Inclusion of stoichiometry in soil food web modelling will also be an important step forward for better understanding of how matter and energy fluxes condition mineralisation of organic matter.

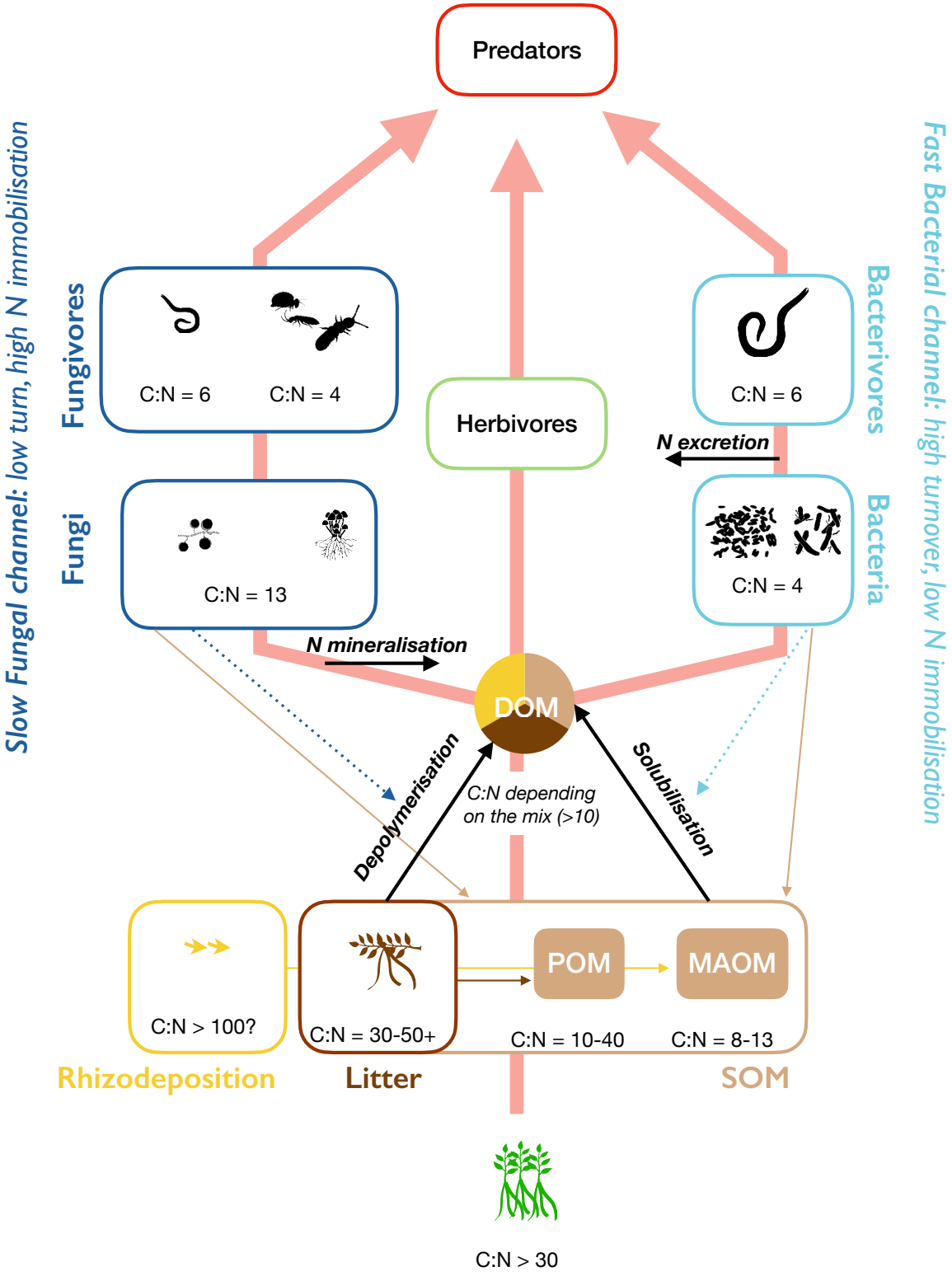

FIGURE 10 Conceptual integration of the fungal:bacterial channels and the spatial compartment approach with some stoichiometric elements

The spatial compartment (but also the equilibrium between microbial groups, with different enzymatic specificities) determines the relative proportions of each basal resource. Fungal and bacterial channels have their specific properties, but are not related with a basal resource in particular (except for mycorrhizal fungi, but it it not apparent on this figure).

2.6. Litter recycling consequences for ecosystem functioning: diving in plant soil feedbacks

Litter decomposition's influence on SOM formation and its modulation by plant strategy is a crucial process in the feedback loop reinforcing spatial fertility gradients (Cornwell et al., 2008; de Vries & Bardgett, 2016; Hobbie, 1992). In Chapter 3, we investigated this question with an original angle by looking at how plant strategy influence plant and microbial litter-derived N recovery, considering not only the fast/slow gradient but also the exploration trade-off. We confirmed that acquisitive species acquired a higher proportion of N from the recycling of their litter, especially "do-it-yourself" species relying less on mycorrhizal partners for soil volume exploration.

Because the litter were produced in hydroponics conditions, we may also have missed a whole range of biotic interactions related to the exploration dimension facilitating litter recycling: endophytes have been shown to enhance litter decomposition (Purahong & Hyde, 2011). More generally, biotic interactions are a key component of global plant-soil feedback (Box 3): beneficial microorganisms are supposed to be less specific than pathogenic ones, leading to higher negative feedbacks for species growing on soil conditioned by conspecific (Ehrenfeld et al., 2005).

Box 3: Defining plant soil feedback

Plant and soil constantly interact through their physical components or via matter and energy exchanges. When a set or a succession of interactions affects the process that triggered it, it is termed a feedback loop (Ehrenfeld et al., 2005). These feedbacks loops can be positive (i.e., directional, that is reinforcing the whole mechanisms) or negative (i.e. stabilising).

Plant-soil feedbacks can be related to biotic and abiotic parameter, at the community scale (e.g for nutrient cycles feedbacks) or the individual/specific scale (e.g. when related to pathogen accumulation).

These biotic interactions, notably belowground, are crucial for understanding community composition. Yet, root systems are often ignored in growth estimation while evaluating plant soil feedback, especially in multispecific conditions, and relatively few species investigated how root traits affect these feedback loops (Cortois et al., 2016).

During this PhD, I also conceived an experiment to evaluate plant soil feedback for 3 species with contrasted root systems (*Anthoxantum odoratum*, *Plantago lanceolata* and *Festuca ovina*). We investigated: (i) whether plant (above *and* belowground traits) would be good predictors of plant soil feedback, especially when (ii) comparing monospecific and pluri-specific conditions, (iii) how plant soil feedback was affected by litter addition (Figure 11). Furthermore, we also wanted to evaluate if accounting for belowground biomass when estimating plant performance would affect the conclusions compared to basing the evaluation on aboveground biomass only.

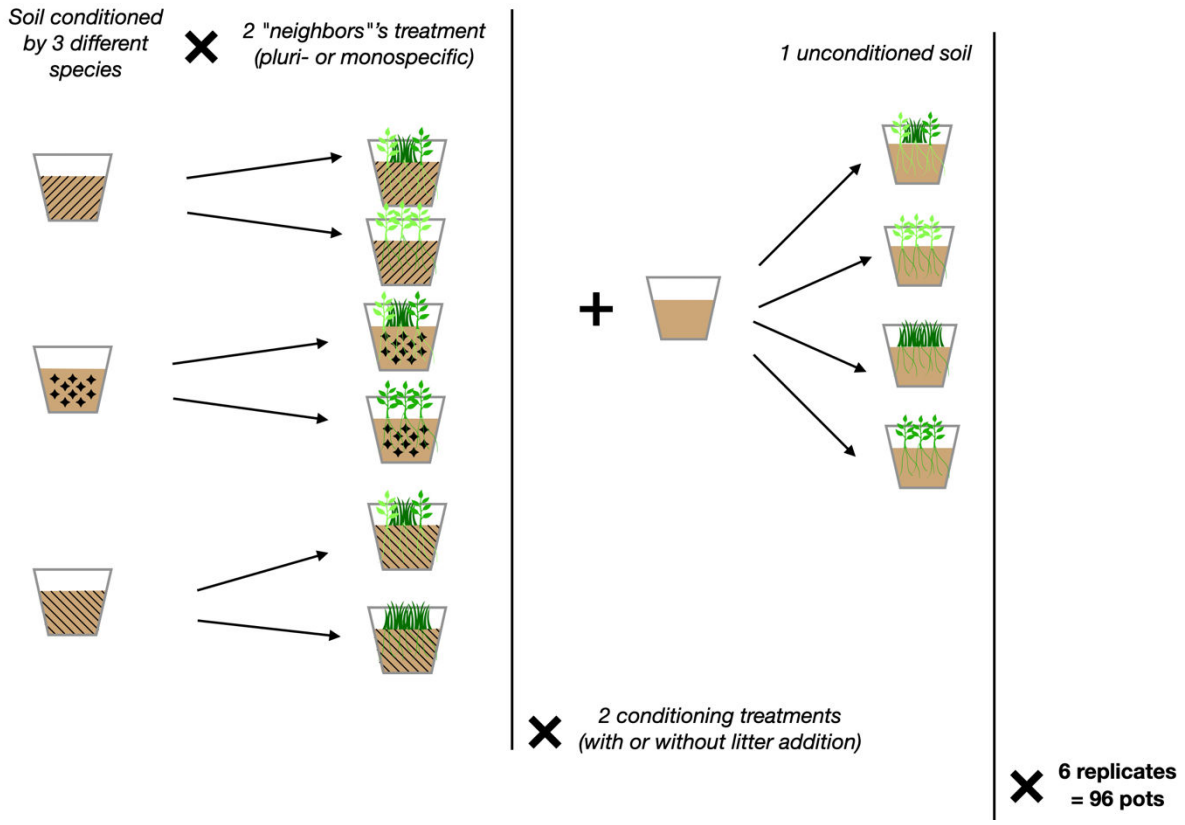

FIGURE 11 Overview of the second experiment's design

To be continued…

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Annexes

1. Chapter 1



FIGURE S1 Coefficient of variation for the traits of interest, calculated for the whole dataset, per functional group and per species.

AGR: Absolute Growth Rate. LDMC: Leaf Dry Matter Content, LNC: Leaf Nitrogen Content, PerColAMF: Degree of AMF Colonisation, PS: Photosynthesis, RCF: Root Cortex Fraction, RDMC: Root Dry Matter Content, RhSoil: Rhisodeposition per gram Soil; RMD: Root Mean Diamater; RNC: Root Nitrogen Content; SLA: Specific Leaf Area; SpLR: Specific Leaf Respiration; SpRh: Specific Rhizodeposition; SpRR: Specific Root Respiration; sr_r : shoot:root ratio; SRL: Specific Root Length

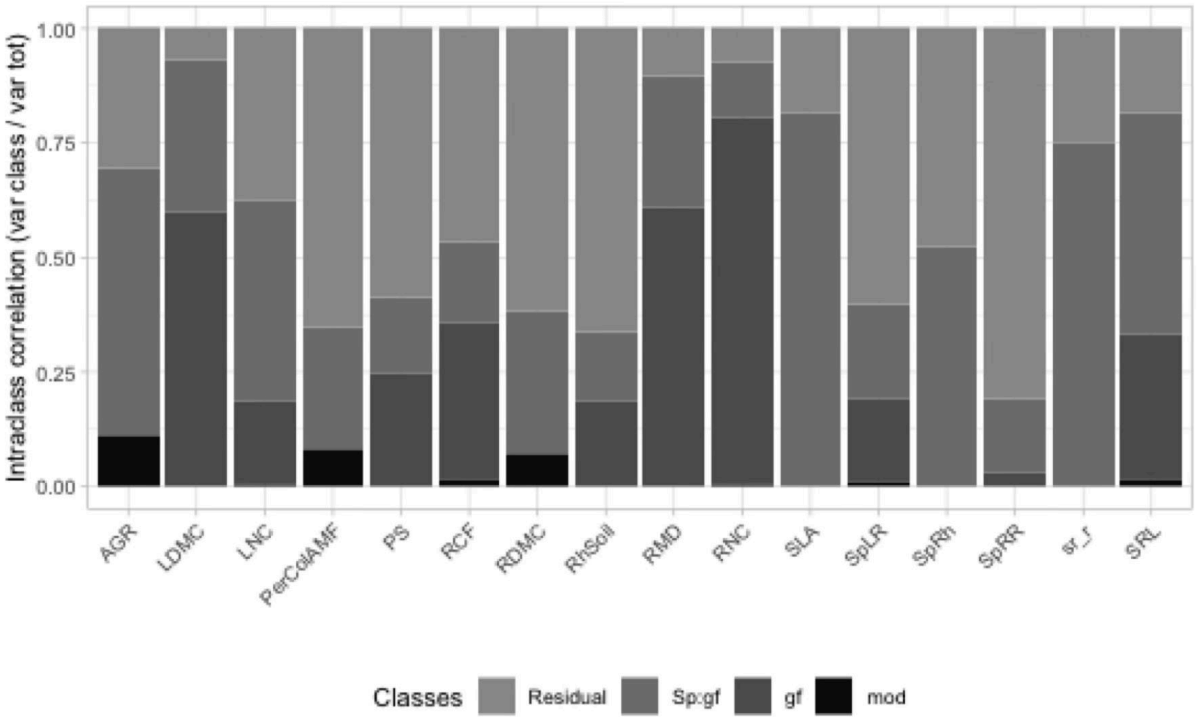

FIGURE S2 Intraclass correlation for the trait of interests

AGR: Absolute Growth Rate. LDMC: Leaf Dry Matter Content, LNC: Leaf Nitrogen Content, PerColAMF: Degree of AMF Colonisation, PS: Photosynthesis, RCF: Root Cortex Fraction, RDMC: Root Dry Matter Content, RhSoil: Rhisodeposition per gram Soil; RMD: Root Mean Diamater; RNC: Root Nitrogen Content; SLA: Specific Leaf Area; SpLR: Specific Leaf Respiration; SpRh: Specific Rhizodeposition; SpRR: Specific Root Respiration; sr_r : shoot:root ratio; SRL: Specific Root Length

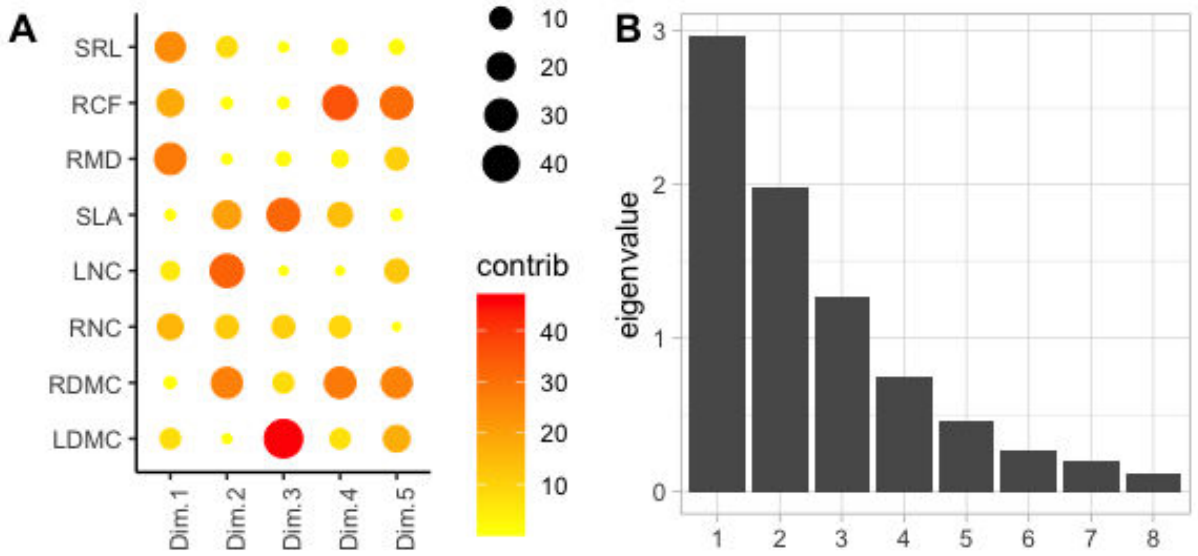

FIGURE S3 Contribution of different variables to PCA axis (A) and dimensions eigenvalues (B)

LDMC: Leaf Dry Matter Content, LNC: Leaf Nitrogen Content, RCF: Root Cortex Fraction, RDMC: Root Dry Matter Content, RMD: Root Mean Diamater; RNC: Root Nitrogen Content; SLA: Specific Leaf Area; SRL: Specific Root Length.

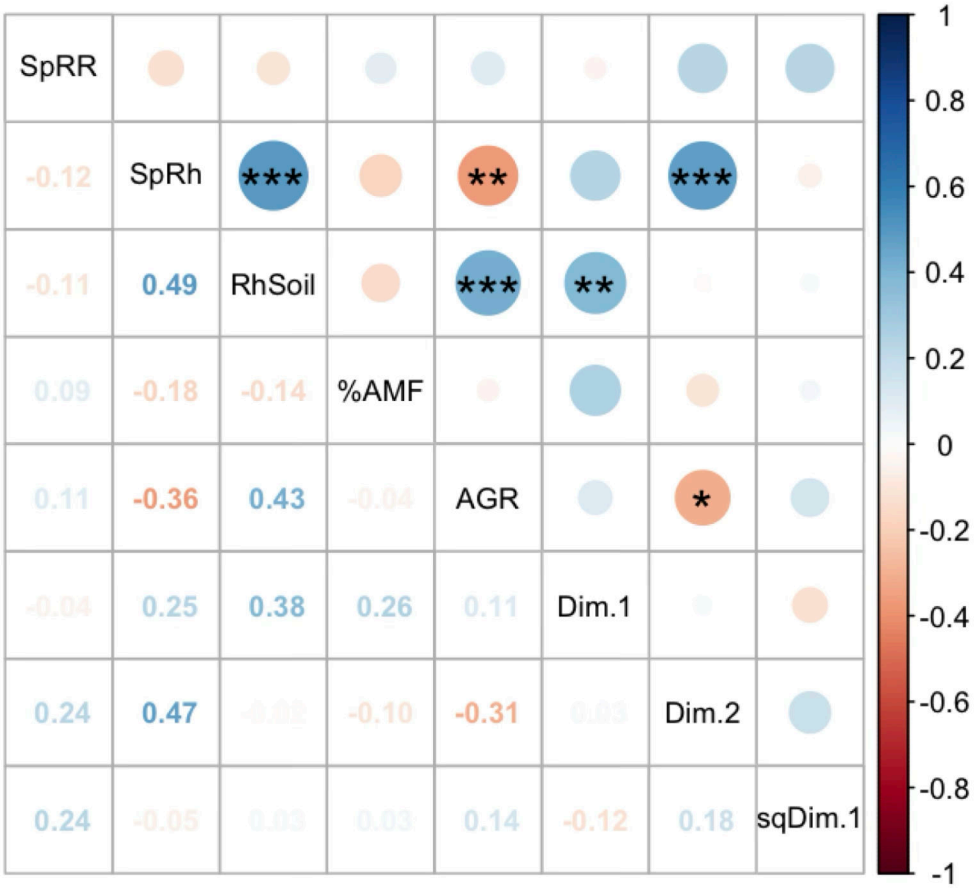

FIGURE S4 Correlation matrix of physiological belowground traits, AGR and PCA axis

AGR: Absolute Growth Rate. LDMC: %AMF: Degree of AMF Colonisation, RhSoil: Rhisodeposition per gram Soil; SpRh: Specific Rhizodeposition; SpRR: Specific Root Respiration; Dim.1 : First PCA axis coordinates, Dim.2: Second PCA axis coordinates; sqDim.1: Dim.1²

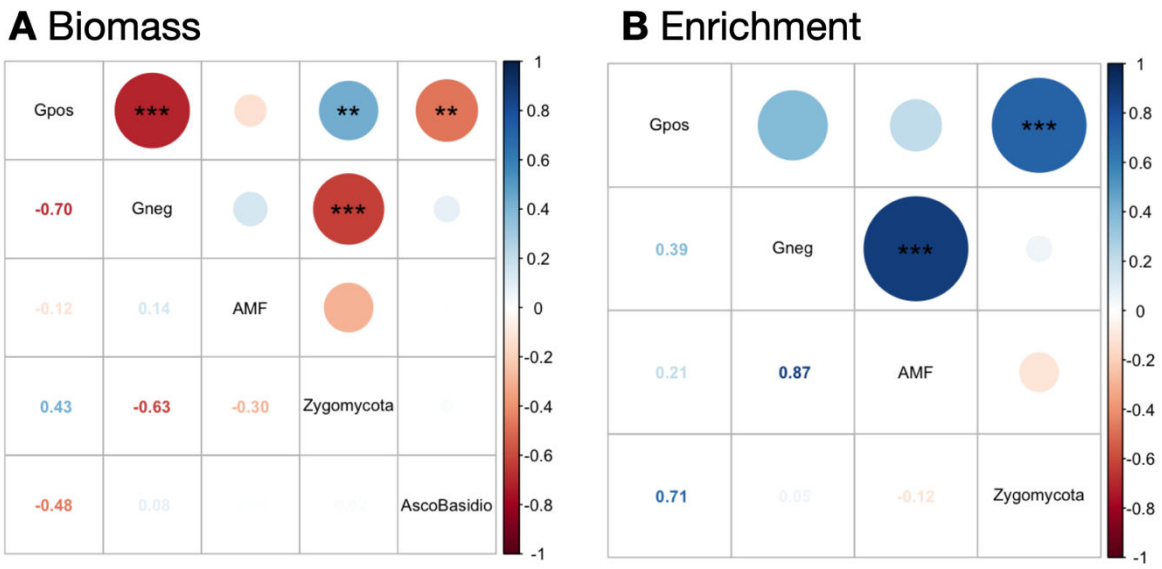

FIGURE S5 Correlation matrix for microbial groups' relative biomass (A) and enrichment (B)

Gpos: Gram positive bacteria; Gneg: Gram negative bacteria; AMF: Arbuscular Mycorrhizal Fungi

TABLE S1 Model selection for physiological traits (ΔAICc < 2)

Formula	df	logLik	AICc	delta	weight	*R2*m	*R2*c
SpRR ~ AGR + Dim.1 + Dim.2 + mod + nod + (1 | Bloc)	8	-99.36	216.65	0.00	0.21	0.27	0.47
SpRR ~ AGR + Dim.1 + Dim.2 + nod + (1 | Bloc)	7	-100.73	216.93	0.28	0.18	0.26	0.46
SpRR ~ AGR + Dim.2 + mod + (1 | Bloc)	6	-102.13	217.34	0.69	0.15	0.25	0.47
SpRR ~ AGR + Dim.2 + (1 | Bloc)	5	-103.30	217.37	0.72	0.14	0.24	0.46
SpRR ~ AGR + Dim.1 + Dim.2 + mod + (1 | Bloc)	7	-101.52	218.51	1.86	0.08	0.25	0.48
SpRh ~ AGR + nod + (1 | Bloc)	5	-86.10	183.07	0.00	0.40	0.35	0.47
SpRh ~ AGR + Dim.1 + nod + (1 | Bloc)	6	-85.75	184.74	1.67	0.17	0.36	0.47
RhSoil ~ AGR + Dim.2 + nod + (1 | Bloc)	6	-87.25	187.74	0.00	0.28	0.27	0.50
RhSoil ~ Dim.2 + nod + (1 | Bloc)	5	-88.85	188.57	0.83	0.18	0.24	0.53
RhSoil ~ AGR + Dim.2 + mod + nod + (1 | Bloc)	7	-86.97	189.62	1.87	0.11	0.28	0.50
PerColAMF ~ Dim.1 + mod + nod + (1 | Bloc)	6	-86.67	186.72	0.00	0.20	0.23	0.23
PerColAMF ~ Dim.1 + mod + (1 | Bloc)	5	-88.06	187.08	0.37	0.17	0.20	0.20
PerColAMF ~ Dim.1 + Dim.2 + mod + (1 | Bloc)	6	-87.56	188.50	1.78	0.08	0.21	0.21
PerColAMF ~ AGR + Dim.1 + mod + nod + (1 | Bloc)	7	-86.42	188.70	1.99	0.08	0.23	0.23

TABLE S2 Model selection for microbial groups' relative biomass (ΔAICc < 2)

formula	df	logLik	AICc	delta	weight	*R2*
Gpos ~ Dim.1 + 1	3	-34.61	76.27	0.00	0.14	0.19
Gneg ~ Dim.1 + RhSoil + 1	4	-27.69	65.74	0.00	0.10	0.24
Gneg ~ 1	2	-30.70	66.04	0.31	0.08	0.00
Gneg ~ RhSoil + 1	3	-29.71	66.76	1.02	0.06	0.09
AMF ~ Dim.1 + PerCol + 1	4	-31.30	72.51	0.00	0.16	0.33
Zygomycota ~ Dim.2 + RhSoil + SpRh + 1	5	-31.08	75.02	0.00	0.13	0.40
Zygomycota ~ RhSoil + 1	3	-34.31	75.66	0.63	0.10	0.24
AscoBasio ~ RhSoil + SpRh + 1	4	-31.71	73.42	0.00	0.06	0.22
AscoBasio ~ Dim.2 + 1	3	-33.45	74.04	0.62	0.04	0.10
AscoBasio ~ RhSoil + 1	3	-33.48	74.11	0.69	0.04	0.10
AscoBasio ~ 1	2	-34.83	74.21	0.79	0.04	0.00
AscoBasio ~ AGR + 1	3	-33.62	74.37	0.96	0.04	0.09
AscoBasio ~ Dim.2 + RhSoil + 1	4	-32.43	74.85	1.44	0.03	0.17
AscoBasio ~ mod + 1	3	-33.89	74.91	1.50	0.03	0.07
AscoBasio ~ mod + RhSoil + 1	4	-32.59	75.19	1.77	0.03	0.16

TABLE S3 Model selection for microbial groups' enrichment (ΔAICc < 2)

formula	df	logLik	AICc	delta	weight	*R2*
firmicutes ~ RhSoil + 1	3	-27.69	62.52	0.00	0.08	0.46
firmicutes ~ RhSoil + SpRh + 1	4	-26.51	63.02	0.50	0.06	0.51
firmicutes ~ mod + RhSoil + 1	4	-26.74	63.48	0.95	0.05	0.50
firmicutes ~ mod + RhSoil + SpRh + 1	5	-25.17	63.49	0.97	0.05	0.56
firmicutes ~ Dim.2 + RhSoil + SpRh + 1	5	-25.21	63.58	1.06	0.04	0.56
firmicutes ~ RhSoil + SpRR + 1	4	-27.05	64.10	1.58	0.03	0.49
Gneg ~ Dim.1 + RhSoil + 1	4	-25.09	60.29	0.00	0.10	0.51
Gneg ~ Dim.1 + RhSoil + SpRh + SpRR + 1	6	-21.89	60.73	0.43	0.08	0.63
Gneg ~ Dim.1 + RhSoil + SpRh + 1	5	-23.89	61.11	0.81	0.07	0.56
Gneg ~ Dim.1 + PerCol + RhSoil + 1	5	-23.99	61.31	1.02	0.06	0.55
Gneg ~ Dim.1 + nod + RhSoil + SpRh + 1	6	-22.54	62.03	1.74	0.04	0.60
Gneg ~ Dim.1 + nod + RhSoil + 1	5	-24.36	62.05	1.76	0.04	0.54
AMF ~ Dim.1 + PerCol + RhSoil + SpRR + 1	6	-12.23	42.47	0.00	0.15	0.67
AMF ~ Dim.1 + RhSoil + SpRR + 1	5	-14.65	43.29	0.82	0.10	0.59
AMF ~ Dim.1 + nod + RhSoil + SpRR + 1	6	-13.18	44.36	1.89	0.06	0.64
Zygomycota ~ RhSoil + 1	3	-28.64	64.54	0.00	0.05	0.28
Zygomycota ~ AGR + RhSoil + 1	4	-27.62	65.47	0.92	0.03	0.34
Zygomycota ~ AGR + nod + 1	4	-27.77	65.76	1.22	0.03	0.33
Zygomycota ~ AGR + nod + PerCol + 1	5	-26.18	65.90	1.35	0.02	0.42
Zygomycota ~ AGR + Dim.1 + 1	4	-27.88	65.97	1.43	0.02	0.33
Zygomycota ~ AGR + 1	3	-29.38	66.03	1.48	0.02	0.23
Zygomycota ~ AGR + Dim.1 + PerCol + 1	5	-26.50	66.54	1.99	0.02	0.40
Zygomycota ~ Dim.1 + 1	3	-29.64	66.54	2.00	0.02	0.21

2. Chapter 2

2.1. Supplementary material & methods

2.1.1 Plant Species selection

We selected plant species based on their *a priori* traits from previous studies.

TABLE S1.1 Plant traits in the literature

Species		Func-tional Group	Family	RGR	SLA		Root Diameter	SRL
Name	*Abbr.*			*Grime & Hunt, 1975 (week^{-1})*	*Grime, 2007 (mm^2·mg^{-1})*	*Sweeny et al., 2021 (mm^2·mg^{-1})*	*Sweeny et al., 2021 (mm)*	*Various (m·g^{-1})*
Nardus stricta (L., 1753)	N.s.	Graminoid	Poaceae	0.71	10.2		0.47	23.72
Festuca ovina (L., 1753)	F.o.	Graminoid	Poaceae	1	10.9			
Anthoxantum odoratum (L., 1753)	A.o.	Graminoid	Poaceae	0.94	27.3	375	0.23	188 - 385.5
Dactylis glomerata (L., 1753)	D.g.	Graminoid	Poaceae	1.31	27.7	404.9	0.24	143.9 - 216,4
Holcus lanatus (L., 1753)	H.l.	Graminoid	Poaceae	2.01	33.5			203.6 - 528 - 593
Campanula rotundifolia (L., 1753)	C.r.	Forb	Campanulaceae	0.81	22.2			
Galium verum (L., 1753)	G.v.	Forb	Rubiaceae	1.2	24.1	584.5	0.21	248.2
Plantago lanceolata (L., 1753)	P.l.	Forb	Plantaginaceae	1.7	22.4	231	0.31	122
Centaurea nigra (L., 1753)	C.n.	Forb	Asteraceae	1.13	26.3	290.7	0.37	77.2
Rumex acetosa (L., 1753)	R.a.	Forb	Polygonaceae	1.71	28.1	401	0.27	31 - 127
Melilotus albus (Medik, 1787)	M.a.	Legume	Fabaceae		21.97			171
Trifolium pratense (L., 1753)	T.p.	Legume	Fabaceae		27.9	391	0.26	190 - 252.1
Lotus corniculatus (L., 1753)	L.c.	Legume	Fabaceae	1.05	29.3	443	0.37	109- 110.2
Medicago sativa (L., 1753)	M.s.	Legume	Fabaceae		33		104.9	
Trifolium repens (L., 1753)	T.r.	Legume	Fabaceae	1.26	38.8	472	0.26	215 - 247.7

2.1.2 Litter production

Litter production

Plants for litter production were grown in a WeissTechnik SGC phytotron under hydroponics conditions, with a nutritive solution (Hoagland, 1920) including 0,2 g/L of 10%-enriched $^{15}KNO_3$. Depending on species' productivity, the growth period lasted between 2 to 4 months, and was followed by a senescence phase, induced by progressively reducing water supply during 1 to 3 weeks. Afterwards, dead biomass was separated into shoots and roots, washed, dried at 40°C and stored for 1 month until the start of the experiment.

Quantity estimate

We estimated the average production of above and below ground litter for a typical temperate grassland, and then adapted this amount to the density of our experiment.

We use the following formula to calculate the AG detrital production DP (Cebrian & Lartigue, 2004):

$$\log_{10}(DP) = 0.08 + \log_{10}(NPP)$$

So, for AG detrital production, we have:

Scurlock et al (2002) estimated above ground (AG) net primary production (ANPP) in grassland to be 508 g.m^{-2}.y^{-1}.

$$DP_{AG} = 10^{-0.08+\log_{10}(508)}$$

```
## [1] "DP_AG = 422.54 g/m2/y"
```

Freschet (2013; Table S1) give an average proportion of AG and below ground (BG) annual litter input of respectively 0.67 and 0.33 for perennial grasslands.

Thus, we can deduce that

$$DP_{BG} = DP_{AG} \cdot \frac{0.33}{0.67}$$

```
## [1] "DP_BG = 208.11 g/m2/y"
```

The density of our pots was N = 7 individuals per pots, so we have $d_{pot} = \frac{N}{S} = 223$ ind m^{-2}. The average density of a grassland is $d_{average} = 2000$ ind m^{-2}.

So we can deduce :

$$\begin{cases} AG_{inputs} & = DP_{AG} \cdot S \cdot \dfrac{d_{pot}}{d_{average}} \\ BG_{inputs} & = DP_{BG} \cdot S \cdot \dfrac{d_{pot}}{d_{average}} \end{cases}$$

2.1.3 Generality on labelling

$^{13}CO_2$ labelling

CO_2 concentration was doubled from 450 ppm to 900 ppm by adding CO_2 produced from the reaction of H2SO4 with a 20% enriched $Na_2{}^{13}CO_3$ solution, following the method of Pang et al. (2021). The CO_2 level was kept between 750 ppm and 900 ppm by regularly adding 10% enriched $^{13}CO_2$ from the same reaction. The chamber was opened between the two labelling days to prevent CO_2 accumulation from nighttime respiration.

Atom percentage excess

Atom percentage excess (APE) is the International System of Units to express the enrichment of a sample (Slater,Preston, Weaver, 2001).

$$APE = (\text{atom}\%)_E - (\text{atom}\%)_B$$

where $(\text{atom}\%)_E$ is the proportion of the rare isotope among the atom of element of interest in the enriched sample, and $(\text{atom}\%)_B$ in a reference baseline.

For ^{15}N labelling, the reference baseline is the mean N-atom% in the same type of sample of the plant-only treatment.

For ^{13}C labelling, the reference baseline is the mean C-atom% of plant grown for litter production, for plant sample. For the litter-only and the control treatment (i.e treatments without plants) we used the mean C-atom% of the same type of sample (i.e., same component for PLFA, for example), sometimes grouped by block or functional group if a statistical difference was found.

Labelling intensity

^{13}C labelling intensity varied across blocks, probably due to variation in soil respiration associated with various pot humidity. Plant respiration and photosynthesis may also have varied. As we added $^{13}CO_2$ when CO_2 concentration dropped below 750 ppm, when the rate of CO_2 absorption was slower, the rate of $^{13}CO_2$ addition was also slower, thus leading to a smaller total addition of label.

We thus decided to calculate relative labelling intensity from the total amount of label added in the labelling chamber in each block, compared to the maximum of the three (i.e. block B). We assumed that the maximum was our labelling goal, that is, 10%.

TABLE S1.2 Block dependant ^{13}C labelling intensity

Block	Labelling Intensity (%)
A	4.6
B	10.0
C	6.6

^{15}N labelling intensity varied across species, due to variation in ^{15}N absorption during litter preparation: legume species have a much lower label content due to its dilution with atmospheric N fixed by their symbionts. ^{15}N labelling intensity corresponds to ^{15}N APE of added litter.

TABLE S1.3 Species dependant ^{15}N labelling intensity

Species	Labelling intensity (%)
F.o.	9.3
A.o.	10.3
D.g.	10.2
H.l.	10.3
G.v.	10.2
P.l.	10.1
C.n.	9.9
R.a.	10.2
M.a.	9.9
T.p.	5.9
L.c.	10.0
M.s.	10.5
T.r.	6.3

2.1.4 Estimation of dissolved organic matter pool size

Total pool size of dissolved organic matter total pool size was estimated by the C-content of unfumigated K_2SO_4 soil extracts.

Rhizodeposits

We did not find a significant enrichment in ^{13}C in this pool, which we attributed to a very high turnover rate. Thus, in order to reflect the existence of the dissolved rhizodeposits pool, we used fumigated extracts enrichment, considering that the ^{13}C had to transit through the dissolved pool. This method provides an overestimation of the pool, but any deviation from the real pool size were corrected by the fine-tuning of preferences parameters to fit real data (see § 1.7.3).

$$DOM_{Rh} = DOC_{tot} \times APE_{F_{extract}} \times \frac{1}{LI_{^{13}C}} \times f$$

where:

- DOM_{Rh} is the rhizodeposit pool (µg · g soil-1),
- DOC_{tot} is the total dissolved organic carbon (µC · g soil-1),
- $APE_{F_{extract}}$ is the ^{13}C enrichment of the fumigated K2SO4 extract,
- LI is the labelling intensity (10%, corrected by block),
- f is the conversion factor from microbial C-content to total microbial biomass (0.4 gC · g-1, Potapov et al, 2022);

Litter

Dissolved litter pool size was estimated from ^{15}N enrichment in the non-fumigated extract.

$$DOM_{Lit} = DOC_{tot} \times APE_{NF_{extract}} \times \frac{1}{LI_{^{15}N}} \times f \times CN_{Lit}$$

where:

- DOM_{Lit} is the pool of litter-derived dissolved organic matter (µg · g soil-1),
- DOC_{tot} is the total dissolved organic carbon (µC · g soil-1),
- $APE_{NF_{extract}}$ is the ^{15}N enrichment of the non-fumigated K2SO4 extract,
- LI is the labelling intensity (10%, corrected by species),
- f is the conversion factor from C-content to total biomass [0.4 gC · g-1]

2.1.5 Microbial biomass estimation

PLFA identification supplementary precisions

Concentrations of phospholipid methyl esters were analysed using a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA) equipped with HP-5 capillary column (30 m x 0.32 mm i.d., film thickness 0.25 µm). The temperature program started with 60 °C (held for 1 min) and increased by 30 °C · min^{-1} to 160 °C followed by 3 °C · min^{-1} to 260 °C. The injection temperature was 250 °C and helium was

used as carrier gas. ^{13}C isotopic signature was assessed at the Centre for Stable Isotope Research and Analysis (University of Göttingen) on a Thermo Finnigan Trace Gas Chromatograph coupled via a GP interface to a Delta V mass spectrometer (Thermo, Bremen, Germany). The GC was equipped with a fused silica capillary column (Agilent DB-5, 30 m, 0.32 mm i.d., film thickness 0.25 µm, Santa Clara, USA).

PLFA attribution

We based our choice of PLFA on the classification by Joergensen (2022).

TABLE S1.4 Assignment of PLFA to different main microbial groups

Component	Group
14:0	Unspecified microbes
i15:0	Gram+ (Firmicutes)
a15:0	Gram+ (Firmicutes)
15:0	Unspecified microbes
i16:0	Gram+ (Firmicutes)
16:1w7	Gram –
16:1w5	AMF
16:0	Unspecified microbes
i17:0	Gram+ (Firmicutes)
cy17:0	Gram –
17:0	Unspecified microbes
18:2w6,9	Ascomycota and Basidiomycota
18:1w9, 18:3w3, 18:2w6t	Zygomycota
18:1w7, 18:1w9t	Gram –
18:0	Unspecified microbes
cy19:0	Gram –
20:4w6	Unspecified microbes
20:0	Unspecified microbes

Conversion from PLFA concentration to PLFA Biomass

To estimate biomass of the different microbial groups, we converted PLFA concentration into microbial C biomass. We used this combination of conversion factors because it was the most consistent with our total estimation of microbial biomass according to the fumigation-extraction method.

However, biomass estimation of saprotrophic fungi was based only on the concentration of 18:2ω6,9, which can lead to underestimating a bit fungal biomass when Zygomycota are dominant (in Litter and Control modalities): the amount of 18:2ω6,9 may be lower while the total amount of fungal PLFAs is stable because the amount of 18:1ω9 is higher.

TABLE S1.5: Overview of Conversion factors combinaisons

PLFA Group	Conversion Factor (µgC nmol-1 PLFA)	Source
Gram+ (Firmicutes)	2.75	Frostegard et Bååth, 1996
Gram –	2.75	Frostegard et Bååth, 1996
AMF	26.32	Olsson et al., 1995
Zygomycota		
Ascomycota and Basidiomycota	107	Joergensen, 2008

Microbial C is then converted into microbial biomass according to the table below with C content (µgC μg^{-1}):

TABLE S1.6: Microbial C content (µgC μg^{-1}), from Potapov 2022 (Supp. Mat.)

Group	Conversion Factor (µgC µg-1)
firmicutes	0.46
Gneg	0.46
AMF	0.41
Zygomycota	0.41
AscoBasio	0.41

We calculated proportion of biomass for each group in each modality (PLFA being measured on a composite sample of the three replicates of one modality), which we multiplied by the total microbial C extracted in the fumigation-extraction protocol (taking into account an extraction efficiency factor $K_{ec} = 0.49$, after Joergensen, 1996) to get the mass of each microbial group for every pot.

2.1.6 Metabolic quotient

The metabolic quotient of soil microbes (qCO_2 [g C-CO_2 g^{-1} Cmicrobial $hour^{-1}$]) was calculated by dividing soil respiration by microbial C biomass obtained by fumigation-extraction, and was standardized to the block-specific temperature (mean atmospheric temperature for the growth period, data from the website https://www.infoclimat.fr/opendata/) using the following equation (Xu et al., 2017):

$$qCO_{2_{pot}} = qCO_{2_{incub}} * Q_{10}^{\frac{T_{field}-T_{incub}}{10}}$$

where $qCO_{2_{pot}}$ and $qCO_{2_{incub}}$ are the qCO_2 for field and incubation conditions, respectively, T_{field} and T_{incub} are the block specific soil temperature (mean across growth period) and the incubation temperature (25 °C), respectively. Q_{10} is the temperature sensitivity coefficient, and a Q_{10} value of 2 was used (Xu et al., 2017).

Mean temperature across the experiment was:

TABLE S1.7 Mean temperature across the experiment for each block

Block	Mean Temperature (°C)
A	19.5
B	19.2
C	18.8

Assuming that bacteria respire twice as much as fungi (Sakamoto et Oba, 1994), we can deduce :

$$\begin{cases} qCO_{2_{bact}} = 2 \cdot qC0_{2_{fungi}} \\ qCO_{2_{fungi}} = qCO_2 \cdot x_{fungi} \end{cases}$$

$$\begin{cases} qCO_{2_{bact}} = 2 \cdot qC0_{2_{fungi}} \\ qCO_{2_{fungi}} = \dfrac{qCO_2}{2 \cdot x_{bacteria} + x_{fungi}} \end{cases}$$

where $x_{bacteria}$ and x_{fungi} are respectively the biomass fraction of each group.

Assuming that there is no difference of respiration rate within bacterial and fungal groups, we also have (where $x_{subgroup} = \frac{subgroup}{group}$), subgroups being Gram+ and Gram- bacteria as well as saprotrophic and AMF fungi :

$$qCO_{2_{subgroup}} = qCO_{2_{group}} \cdot x_{subgroup}$$

2.1.7 Resource preference and trophic interaction matrices

Overview of the construction of the trophic interaction matrix

The trophic interaction matrix was constructed as the product between the resource biomass and resource preferences matrices. The parameters for soil fauna are documented in the literature (see §1.7.2), but information on microbial preferences is lacking. We therefore used stable isotope probing (SIP) from our ^{13}C living plant pulse labelling and ^{15}N litter continuous labelling to estimate those resource preferences. Because of the different elemental nature and the difference of labelling type, we had to use these data differently.

^{13}C PLFA-SIP was used to estimate relative preferences for SOM and rhizodeposits (§1.7.3.1) by comparing the proportion of rhizoflux (model output) in each microbial node inflow to proportion of rhizodeposits in PLFA-C (measured).

^{15}N PLFA-SIP was used to estimate relative consumption (i.e. interaction strength, §1.7.3.2) of SOM and litter, at the scale of total microbial biomass and not single microbial groups.

Resource preference matrix for soil fauna

Soil fauna feeding preferences were determined based on Potapov et al. (2022), with 1 indicating the principal resource, while 0.2 indicates a secondary resource (Table S1.9).

Compared to Potapov et al. (2022), our preference matrix includes a few modifications:

- Rhizodeposition was added as basal resources and algae were ignored,
- The microbial compartment was split into four subgroups : Gram+ and Gram- bacteria as well as saprotrophic and AMF fungi,
- The classical separation between epedaphic and hemeidaphic Collembola was used, instead of Algivores vs Detritivores,
- a preference factor of 10^{-9} was added for groups that were present while none of their principal or secondary resources were available to reflect possible use of this resource (e.g.: phytophagous nematodes can feed on fungal hyphae in absence of plants).

Microbial preference/interaction matrix fine tuning

Microbial preferences of rhizodeposition compared to SOM

We calculated enrichment for each microbial group by the mean of the APE of each group's PLFAs, weighted by their concentrations, considering the number of carbon content of each PLFA ($n_{C_{PLFA_i}}$).

$$APE_{group} \times Concentration_{group} = \sum_{PLFA_{group}} APE_{PLFA_i} \times Concentration_{PLFA_i} \times n_{C_{PLFA_i}}$$

where $Concentration_{group} = \sum_{PLFA_{group}} Concentration_{PLFA_i}$.

So,

$$APE_{group} = \frac{\sum_{PLFA_{group}} APE_{PLFA_i} \times Concentration_{PLFA_i} \times n_{C_{PLFA_i}}}{\sum_{PLFA_{group}} Concentration_{PLFA_i}}$$

and

$$\%Rhizo_{group} = APE_{group} \times \frac{1}{10\%}$$

with $\%Rhizo_{group}$ the proportion of carbon from rhizodeposits in each microbial group and 10% is the labelling intensity (there is no need to correct for differences between block, as PLFA measurements were pooled by modality).

To determine preference of microbial groups for SOM we used different combinations for Gram+ / Gram- bacteria and saprotrophic fungi, to find that the parameter giving output graphically (see below) most similar to our data were 0.002 for Gram- bacteria and saptrophic fungi but 0.02 for Gram+ bacteria. This is consistent with other findings that Gram+ bacteria are often less related to recent photosynthates than other microbial groups (Balasooriya et al., 2012; Chaudhary & Dick, 2016; Fanin et al., 2019).

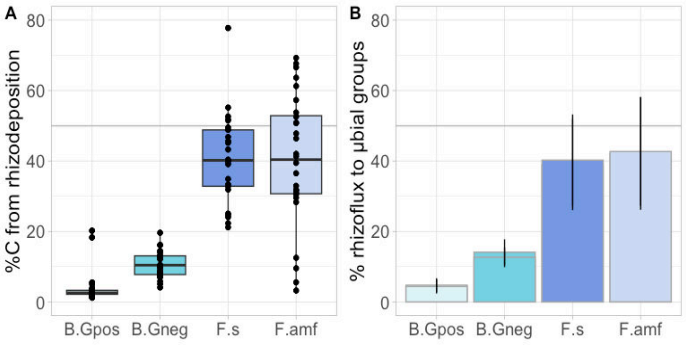

FIGURE S1.1: Comparison of ^{13}C-based estimation of microbial feeding on rhizodeposition (A) and model outputs (B)

Microbial consumption of litter compared to SOM

Hypothesis

Relative microbial preference for SOM and litter was assessed from ^{15}N enrichment of microbial biomass, considered to reflect microbial consumption of both sources, under the following hypotheses:

- Nitrogen decomposed from both litter and SOM sources is completely absorbed by microbes
- CUE is identical for both sources

With:

- L the proportion of flux coming from litter,
- S the proportion of flux coming from SOM,
- N_{lit_μ}, the proportion of nitrogen in the microbial biomass coming from litter,
- N_{SOM_μ}, the proportion of nitrogen in the microbial biomass coming from SOM,
- N_{lit}, the proportion of nitrogen in the litter,
- C_{lit}, the proportion of carbon in the litter,
- N_{SOM}, the proportion of nitrogen in SOM,
- C_{SOM}, the proportion of carbon in SOM,

Then, we have:

$$\frac{N_{lit_\mu}}{N_{SOM_\mu}} = \frac{L \times \frac{N_{lit}}{C_{lit}}}{S \times \frac{N_{SOM}}{C_{SOM}}}$$

$$\Leftrightarrow \frac{L}{S} = \frac{\frac{N_{lit}}{C_{lit}}}{\frac{N_{SOM}}{C_{SOM}}} \times \frac{N_{SOM_\mu}}{N_{lit_\mu}}$$

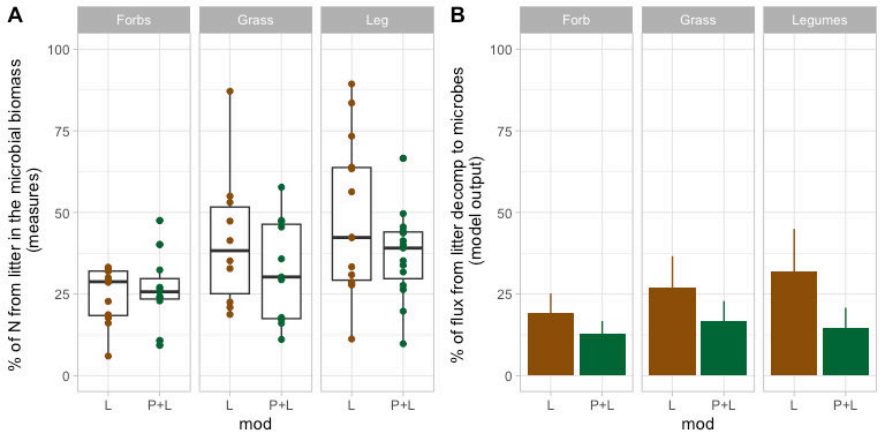

FIGURE S1.2 Comparison of litter-derived microbial biomass (A) and model outputs (B)

Because it was variable across plant species, we decide to calculate one coefficient per pot.

2.1.8 Overview of fluxing inputs

Preference matrix in the soil food web

NAs for dissolved litter reflects the fact that their value was directly filled in the interaction matrix instead of being the product of preference × biomass.

TABLE S1.8 Preference matrix with consumers as lines

Group	Abbr.	P. FR	P dL	P. rL	P. lL	P. Rh	S	B. Gpos	B. Gneg	F. s	F. amf	Ne. PhP	Ne. fPh	Ne B	Ne F	Ne. Omn	Ne P	Me	Cla. Epe	Cla. Hem
Resources: Fine roots	*P.FR*																			
Resources: Dissolved litter	*P.dL*																			
Resources: Root litter	*P.rL*																			
Resources: Leaf litter	*P.lL*																			
Resources: Rhizodeposition	*P.Rh*																			
Resources: Soil organic matter	*S*																			
Bacteria:Gram+	*B.Gpos*		NA			1	0.02													
Bacteria:Gram-	*B.Gneg*		NA			1	0.002													
Fungi: saprotrophic	*F.s*		NA			1	0.002													
Fungi:AMF	*F.amf*		NA			1	1e-09													
Nematoda: Phytoparasites	*Ne. PhP*	1								1e-09	1e-09									
Nematoda: Facultative phytophages	*Ne. fPh*	1								0.5	0.5									
Nematoda: Bacterivores	*Ne.B*							1	1											
Nematoda: Fungivores	*Ne.F*									1	1									
Nematoda: Omnivores	*Ne. Omn*							1	1			1	1	1	1	1	0.5			
Nematoda: Predators	*Ne.P*											1	1	1	1	1	1			
Mesostigmata	*Me*											0.5	0.5	0.5	0.5	0.5	0.5	0.5	1	1
Collembola: Epedaphic	*Cla. Epe*				0.5			0.5	0.5	1	1									
Collembola: Hemiedaphic	*Cla. Hem*			1	1			0.5	0.5	1	1									

TABLE S1.9 Overview of inputs

Group	Metabolic Needs				Biomass				Absorption efficiency			
	C	L	P	P+L	C	L	P	P+L	C	L	P	P+L
B.Gneg	711.57 ± 334	672.16 ± 528	837.68 ± 325	806.12 ± 358	13.2 ± 51	12.6 ± 41	13.1 ± 41	13.2 ± 51	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
B.Gpos	1574.35 ± 922	1628.61 ± 815	1624.79 ± 630	1618.35 ± 555	19.4 ± 71	20.2 ± 61	18.1 ± 51	18.9 ± 71	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Cla.Epe	0.11 ± 0	0.03 ± 0	0.2 ± 0	0.21 ± 0	0.2 ± 01	0 ± 01	0.3 ± 01	0.3 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Cla.Hem	0.15 ± 0	0.24 ± 1	0.18 ± 0	0.32 ± 0	0.1 ± 01	0.5 ± 21	0.1 ± 01	0.2 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
F.amf	0.92 ± 1	0.89 ± 0	861.41 ± 353	896.76 ± 346	30.6 ± 111	32.9 ± 111	30.8 ± 101	34.1 ± 131	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
F.s	2235.58 ± 1121	2745.55 ± 1601	2327.58 ± 1188	2540.56 ± 1239	35 ± 131	43 ± 141	49.6 ± 161	56.1 ± 191	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Me	0.01 ± 0	0.01 ± 0	0.02 ± 0	0.02 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.B	0.49 ± 0	0.52 ± 0	0.49 ± 1	0.54 ± 1	0.1 ± 01	0.2 ± 01	0.2 ± 01	0.2 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.F	0.01 ± 0	0.02 ± 0	0.01 ± 0	0.03 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.Omn	0.09 ± 0	0.03 ± 0	0.01 ± 0	0 ± 0	0.1 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.P	0 ± 0	0.01 ± 0	0 ± 0	0.01 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.PhP	0 ± 0	0.01 ± 0	0.02 ± 0	0.03 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
Ne.fPh	0 ± 0	0.01 ± 0	0.01 ± 0	0.01 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	0.11 ± 0	0.11 ± 0	0.11 ± 0	0.11 ± 0
P.FR	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 01	0 ± 01	46.1 ± 371	60.6 ± 321	0 ± 0	0 ± 0	0.11 ± 0	0.11 ± 0
P.Rh	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 01	0 ± 01	0 ± 01	0 ± 01	1 ± 0	1 ± 0	1 ± 0	1 ± 0
P.dL	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 01	2 ± 11	0 ± 01	0.4 ± 11	1 ± 0	1 ± 0	1 ± 0	1 ± 0
P.lL	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 01	37 ± 01	0 ± 01	37 ± 01	0 ± 0	0.12 ± 0	0 ± 0	0.12 ± 0
P.rL	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 01	18.4 ± 01	0 ± 01	18.4 ± 01	0 ± 0	0.12 ± 0.01	0 ± 0	0.12 ± 0.01
S	0 ± 0	0 ± 0	0 ± 0	0 ± 0	12.9 ± 61	9 ± 41	10.9 ± 41	9.1 ± 51	1 ± 0	1 ± 0	1 ± 0	1 ± 0

2.1.9 Outliers' policy

We excluded extreme outliers from our data. Below are the proportion of pots excluded for each table (fluxes, plant traits, litter properties).

TABLE S1.10 Extremes outliers for fluxes

Flux	Ext. Outliers Count	N	PerExtremes (%)
Herbivory	3	84	3.57
Rhizoflux	0	84	0.00
Detritivory	0	78	0.00
Decomposition	1	129	0.78
Bacterivory	5	129	3.88
Microbivory	3	129	2.33
Carnivory	4	129	3.10
Total	1	129	0.78
Fungivory	1	129	0.78
SOM decomp.	2	129	1.55

TABLE S1.11 Extremes outliers for plant traits

Trait	Ext. Outliers Count	N	PerExtremes (%)
PerColAMF	0	84	0.00
R_resp	0	84	0.00
PS	1	84	1.19
AGR	0	84	0.00

TABLE S1.12 Extremes outliers for litter properties

Trait	Ext. Outliers Count	N	PerExtremes (%)
P	0	78	0.00
Mn	5	78	6.41
CNratio	0	78	0.00
Ca	0	78	0.00
Mg	0	78	0.00

2.2. Supplementary Results

2.2.1 Models comparing biomass

Only coefficients with 95% confidence intervals not intersecting with 0, or with estimates higher than 0.2 and with model R^2c higher than 10% are presented.

TABLE S2.1 Overview of treatment effect on node biomass

Node	Formula	Parameter	Estimate	CI_low	CI_high	R^2m	R^2c
Dissolved SOM	P + L + (1 | Block) + (1 | Sp)	L	-0.4877	-0.784	-0.1915	4.3	49.7
Saprotrophic Fungi	P + L + (1 | Block) + (1 | Sp)	P	0.7805	0.5338	1	9.6	71.1
Saprotrophic Fungi	P + L + (1 | Block) + (1 | Sp)	L	0.3767	0.1328	0.6201	9.6	71.1
AMF	P + L + (1 | Block) + (1 | Sp)	L	0.2824	0.0099	0.555	1.3	63.5
Strict phytophagous Nematodes	P + L + (1 | Block) + (1 | Sp)	P	0.6349	0.1437	1.1	6.7	7.7
Facultative phytophagous Nematodes	P + L + (1 | Block) + (1 | Sp)	P	0.2511	-0.1897	0.6933	11.1	11.2
Facultative phytophagous Nematodes	P + L + (1 | Block) + (1 | Sp)	L	-0.5345	-0.973	-0.0951	11.1	11.2
Fungivorous Nematodes	P + L + (1 | Block) + (1 | Sp)	P	0.2345	-0.1735	0.6392	3.4	10.3
Fungivorous Nematodes	P + L + (1 | Block) + (1 | Sp)	L	0.4177	0.0106	0.8227	3.4	10.3
Omnivorous Nematodes	P + L + (1 | Block) + (1 | Sp)	P	-0.8741	-1.5378	-0.233	12.8	41.6
Predatory Nematodes	P + L + (1 | Block) + (1 | Sp)	L	0.5024	-0.4307	1.4	17	17
Mesostigmata	P + L + (1 | Block) + (1 | Sp)	P	0.4324	0.0175	0.8483	3.4	12.5
Epedaphic Springtails	P + L + (1 | Block) + (1 | Sp)	P	0.7484	0.2916	1.2	12.6	23.9

2.2.2 Litter properties correlation

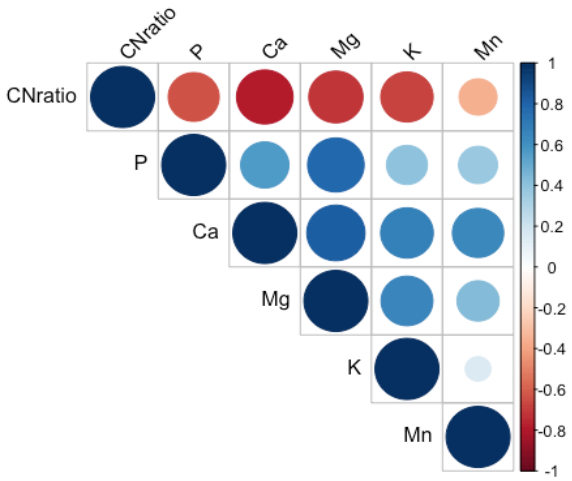

FIGURE S2.1 Correlation matrix of litter properties

2.2.3 Complete model selection output (complement to Figure 4)

In this section we present the whole list of models selected by the criterion delta-AIC < 2 and vif < 5.

TABLE S2.2 Overview of all models selected for litter properties

Flux	Formula	Int.	Pl	CN ratio	K	Mg	Mn	P	df	logLik	AICc	delta	weight
Total	Pl + (1 | Bloc)	-0.3	+						4	-84.4	177.5	0	0.3
Total	P + Pl + (1 | Bloc)	-0.3	+					0.2	5	-83.7	178.5	1	0.2
Predation	Pl + (1 | Bloc)	-0.3	+						4	-92	192.7	0	0.3
Fungivory	Pl + (1 | Bloc)	-0.7	+						4	-76.8	162.2	0	0.5
SOM decomp.	Pl + (1 | Bloc)	0.4	+						4	-82.4	173.5	0	0.2
SOM decomp.	P + Pl + (1 | Bloc)	0.4	+					-0.2	5	-81.5	174	0.4	0.2
SOM decomp.	Mg + Pl + (1 | Bloc)	0.4	+			-0.2			5	-81.6	174.1	0.6	0.1
SOM decomp.	CNratio + Pl + (1 | Bloc)	0.4	+	0.2					5	-81.6	174.3	0.7	0.1
Litter decomp.	Mn + P + Pl + (1 | Bloc)	0.5	+				-0.3	0.5	6	-74	161.3	0	0.6
Rhizoflux	P + (1 | Bloc)	0	NA					0.4	4	-49	107.4	0	0.2
Rhizoflux	Mg + (1 | Bloc)	0	NA			0.3			4	-50	109.2	1.8	0.1
Rhizoflux	K + Mg + (1 | Bloc)	0	NA		-0.4	0.6			5	-48.7	109.4	2	0.1

TABLE S2.3 Overview of all models selected for plant traits

Flux	Formula	(Intercept)	L	AGR	R_resp	df	logLik	AICc	delta	weight
Total	AGR + (1 | Block)	0.1		0.2		4	-77.1	162.9	1	0.2
Predation	L + (1 | Block)	-0.2	+			4	-85.3	179.2	1.2	0.2
Fungivory	L + (1 | Block)	-0.2	+			4	-84.2	177.1	0	0.3
SOM decomp.	L + (1 | Block)	0.4	+			4	-69.7	148.2	0	0.7
Litter decomp.	R_resp + (1 | Block)	-0.1			0.6	4	-31.2	72.6	0	0.5
Rhizoflux	AGR + (1 | Block)	0		0.3		4	-82.8	174.3	0.5	0.2
Rhizoflux	AGR + L + (1 | Block)	0.2	+	0.3		5	-82.1	175.4	1.6	0.1

2.2.4 Influence of plant strategy on *f:b* ratios

TABLE S2.4 Selected models for *f:b* channel ratios explained by plant traits

formula	(Intercept)	L	nod	AGR	R_resp	df	logLik	AICc	delta	weight
fb_Microbivory ~ (1 | Block)	1.4					3	-88.2	182.9	0	0.3
fb_Microbivory ~ L + (1 | Block)	1.3	+				4	-87.5	183.6	0.7	0.2
fb_Microbivory ~ AGR + (1 | Block)	1.4			0.2		4	-87.8	184.4	1.5	0.1
fb_SOM decomp. ~ nod + (1 | Block)	-0.6		+			4	-59.5	127.6	0	0.2
fb_SOM decomp. ~ R_resp + (1 | Block)	-0.8				-0.2	4	-60.3	129.4	1.7	0.1
fb_SOM decomp. ~ nod + R_resp + (1 | Block)	-0.7		+		-0.2	5	-59.2	129.6	1.9	0.1
fb_Litter decomp. ~ R_resp + (1 | Block)	-0.7				-0.3	4	-28.5	67	1.9	0.1
fb_Rhizoflux ~ nod + (1 | Block)	0.2		+			4	-80	168.8	0	0.2
fb_Rhizoflux ~ L + nod + (1 | Block)	0.1	+	+			5	-79.1	169.3	0.5	0.2
fb_Rhizoflux ~ nod + R_resp + (1 | Block)	0.3		+		0.3	5	-79.2	169.5	0.7	0.1
fb_Rhizoflux ~ L + nod + R_resp + (1 | Block)	0.1	+	+		0.3	6	-78.3	170.2	1.4	0.1

TABLE S2.5 Selected models for *f:b* channel ratios explained by litter properties

formula	(Intercept)	Pl	P	Mn	Mg	df	logLik	AICc	delta	weight
fb_Microbivory ~ Pl + (1 | Bloc)	0.5	+				4	-72.7	154.1	0	0.3
fb_Microbivory ~ P + Pl + (1 | Bloc)	0.5	+	0.2			5	-72	155	0.9	0.2
fb_SOM decomp. ~ Mn + Pl + (1 | Bloc)	1.1	+		-0.2		5	-60.8	132.6	0	0.3
fb_SOM decomp. ~ Mg + Pl + (1 | Bloc)	1.1	+			-0.2	5	-61.1	133.2	0.6	0.2
fb_Litter decomp. ~ Mn + Pl + (1 | Bloc)	0.8	+		-0.2		5	-60.5	132	0	0.3
fb_Litter decomp. ~ Mg + Pl + (1 | Bloc)	0.7	+			-0.2	5	-60.8	132.5	0.6	0.2
fb_Rhizoflux ~ P + (1 | Bloc)	0.1		-0.5			4	-46.8	102.8	0	0.4

2.2.5 Total fluxes to bacteria vs total fluxes to fungi

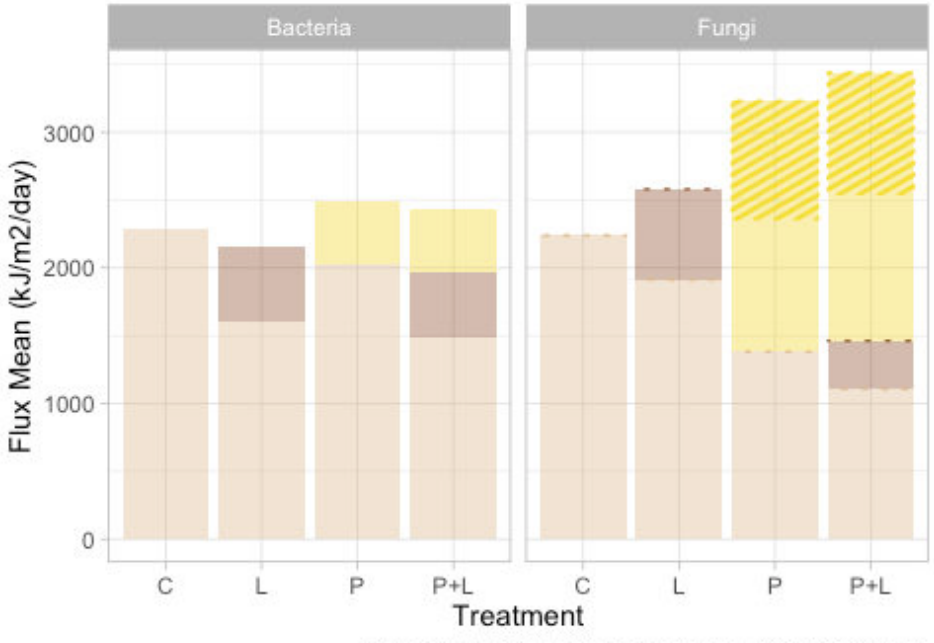

FIGURE S2.2 Overview of fluxes to bacteria vs fluxes to fungi.

C: Control, L: Litter-only, P: Plant, P+L: Plant+Litter. Color indicates flux origin – SOM: light brown. Litter: brown, Rhizodeposition: yellow. Stripes indicates fluxes to AMF.

2.2.6 Contributors to fungivory and bacterivory

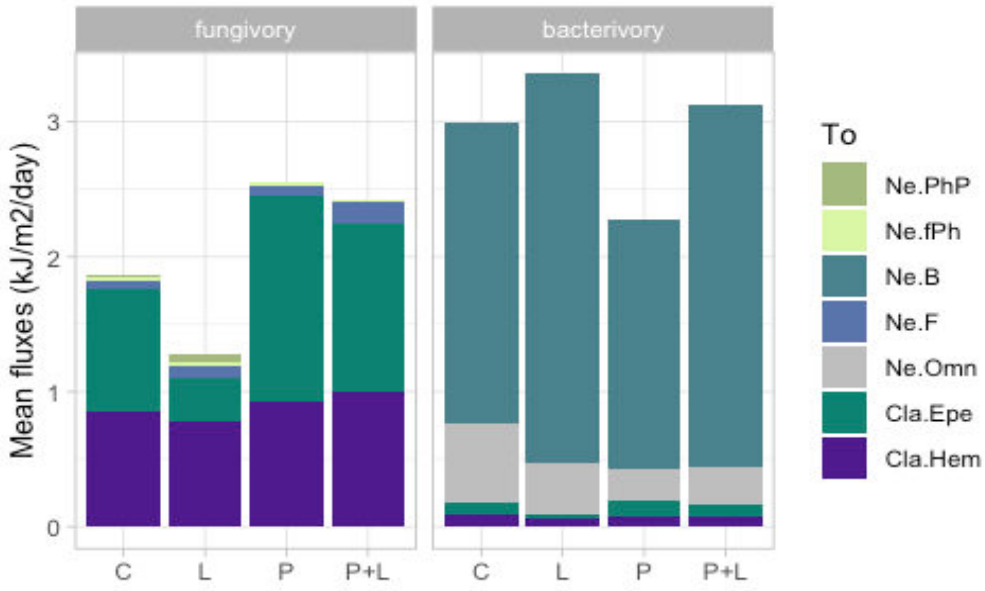

FIGURE S2.3 Contribution to fungivory and bacterivory.

Color indicates flux destination (consumer). Ne: nematodes – PhP: phytophageous, fPh: facultative phytogapheous, B: bacterivorous, F: fungivorous, Omn: omnivorous. Cla: collembola – Epe: epedaphic, Hem: hemiedaphic.

2.2.7 Enrichment of microarthropods groups

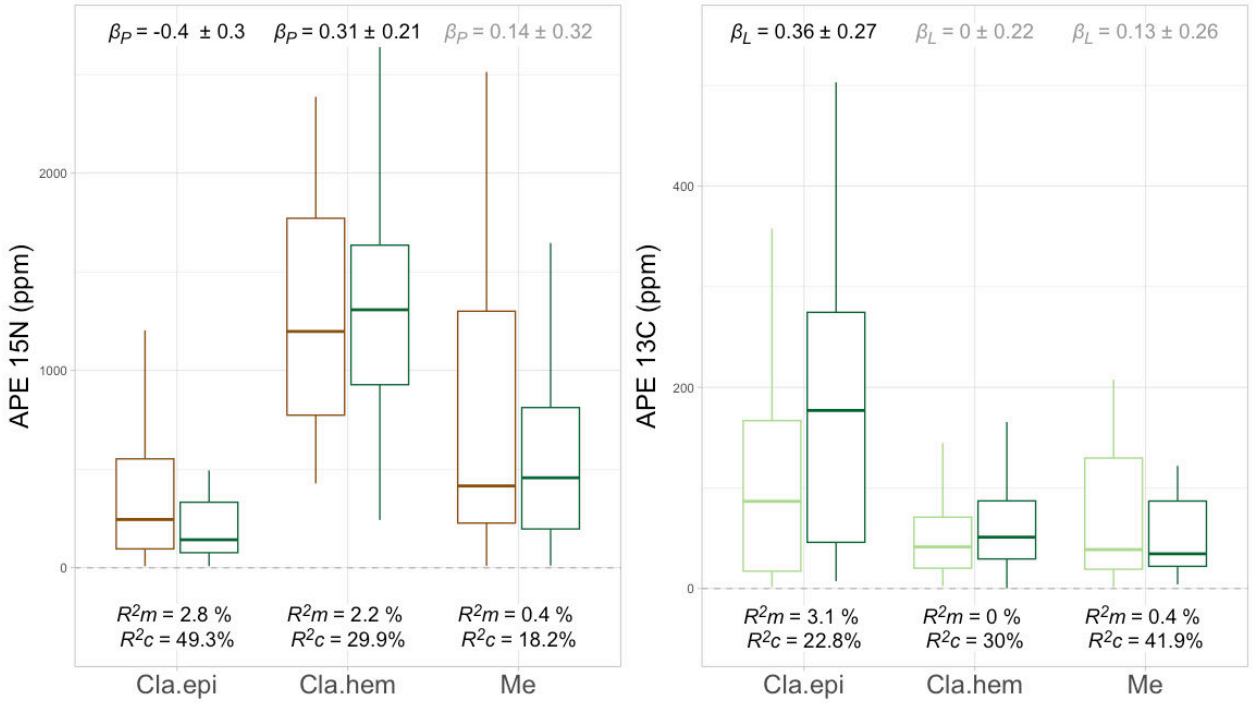

FIGURE S2.4 Enrichment of microarthropod groups.

Me: mesostigmata, Cla: collembola – Epe: epedaphic, Hem: hemiedaphic. Color reflects treatment – brown: litter-only, dark green: plant+litter, light green: plant-only.

3. Chapter 3

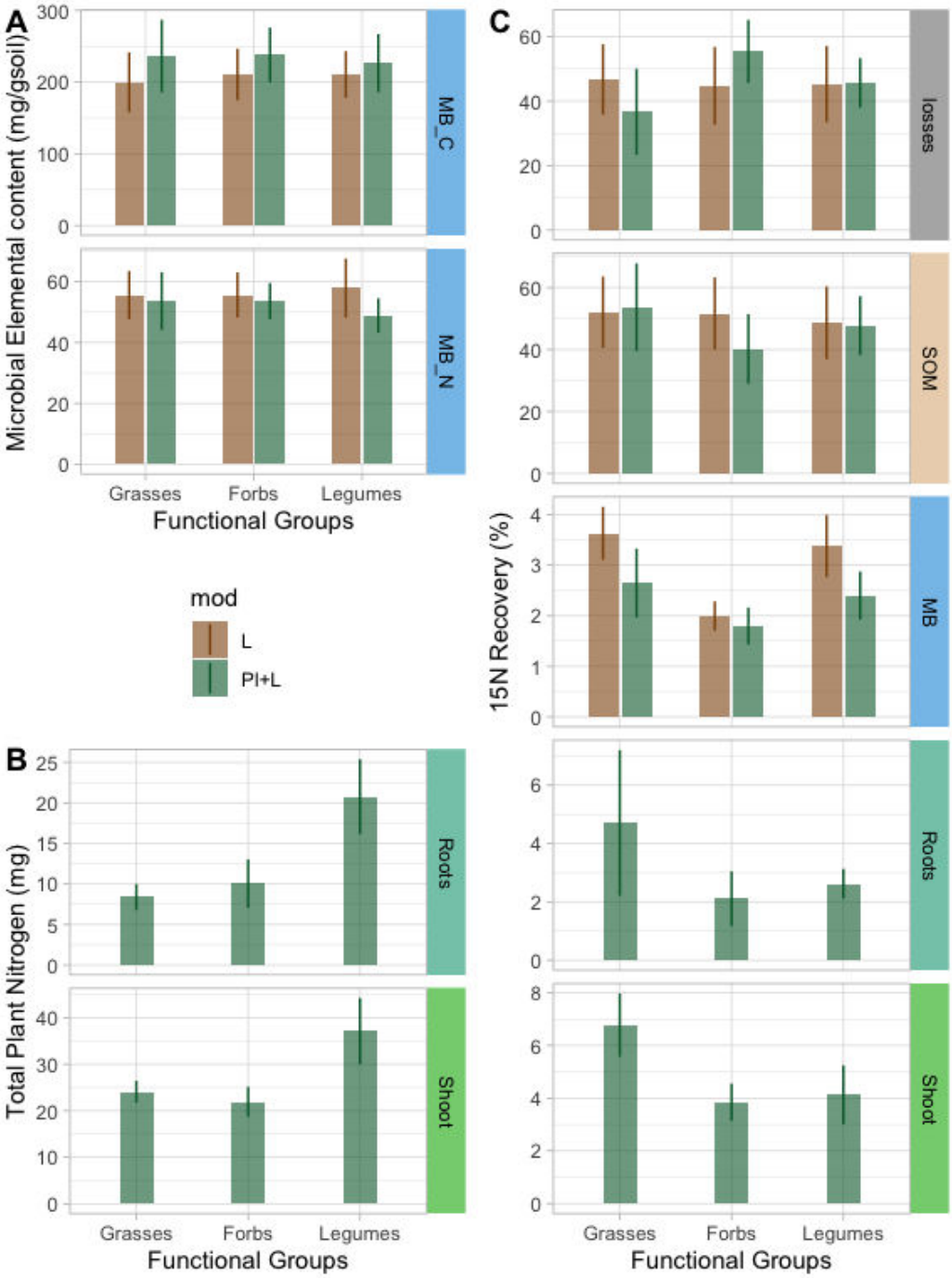

FIGURE S1 Overview of microbial elemental content (A), total plant nitrogen. (B) and 15N recovery (C) per functional group.

Values indicated are mean and its 95% confidence interval.

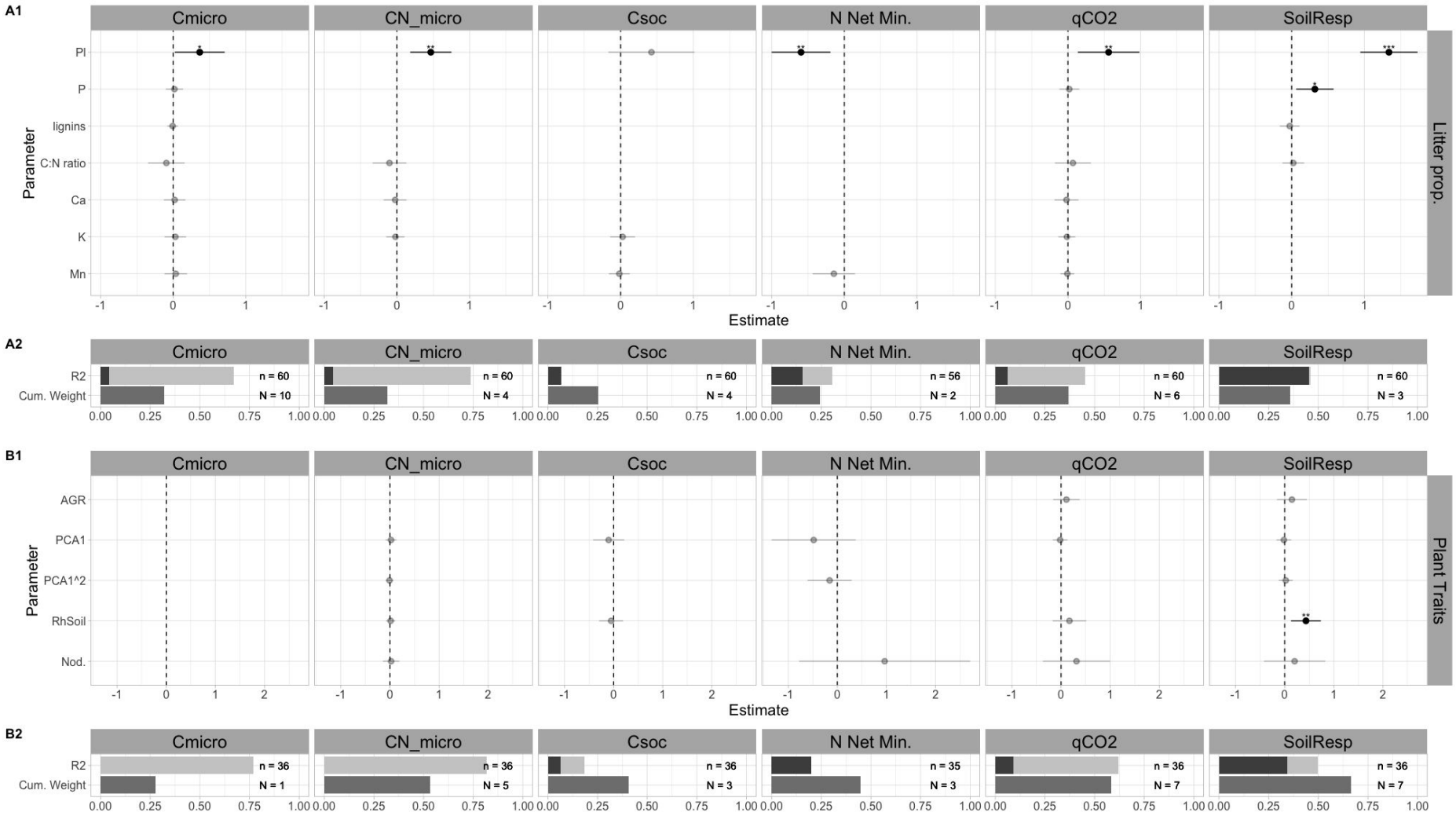

FIGURE S2 Parameters and properties of averaged models explaining microbial biomass and activity by plant strategy

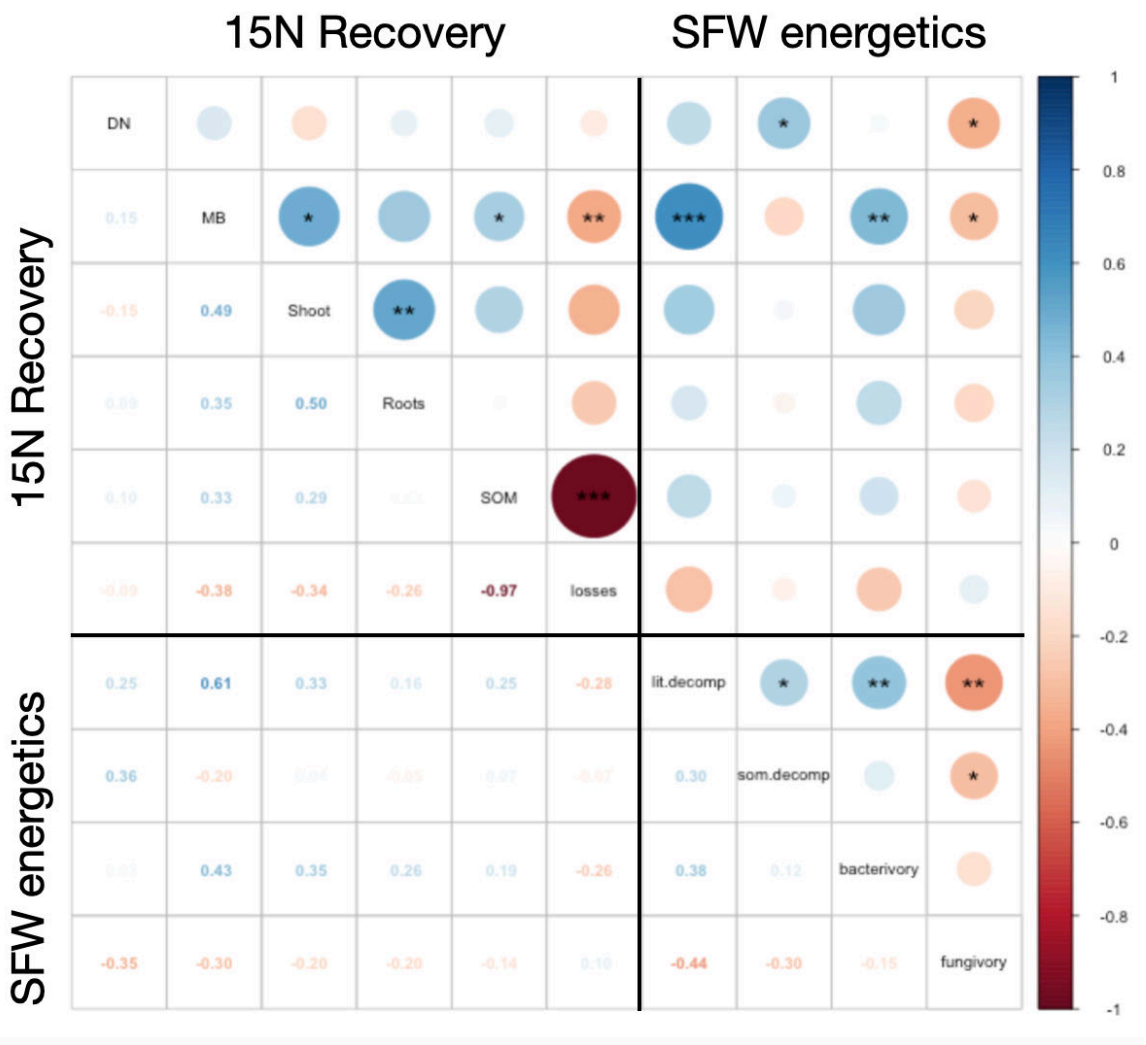

FIGURE S3 Correlation matrix with litter-derived N recovery patterns and soil food webs' energy fluxes

Résumé general / Abstract

Les organismes du sol (plantes, faune, microbes) ont été l'objet d'un regain d'attention au cours des dernières années. Les interactions trophiques entre ces organismes participent largement au fonctionnement des écosystèmes, par exemple via leur impact sur les cycles biogéochimiques. Dans ce manuscrit, nous avons étudié comment la stratégie d'acquisition des ressources des producteurs primaires (les plantes) affecte la quantité et la qualité de deux ressources basales : la litière et les rhizodépôts (Chapitre 1) ; nous avons ensuite partitionné l'importance de ces deux ressources pour les réseaux trophiques du sol (Chapitre 2) et évalué leur impact sur le recyclage de l'azote issu de la décomposition de la litière (Chapitre 3). Nous avons utilisé l'espace économique des plantes comme cadre théorique pour décrire les stratégies d'acquisition. Il inclut deux gradients indépendants : (i) le gradient lent/rapide qui oppose les espèces acquisitives à croissance rapide et métabolisme efficace, aux espèces conservatives à croissance lente et à forte longévité, et (ii) le gradient d'exploration, qui oppose les espèces « do-it-yourself » avec un système racinaire morphologiquement efficace aux espèces « délégatrices » qui dépendent de la mycorhization. Une expérience en mésocosme avec 15 espèces prairiales aux stratégies contrastées, croisant l'ajout de litière et la présence de plantes vivantes a été mise en place. Nous avons utilisé un marquage isotopique pour suivre le devenir du carbone issu de la rhizodéposition et de l'azote issu de la décomposition de la litière dans différents compartiments (les plantes, le sol, et les communautés de faune et de microbes).

Plus spécifiquement, dans le premier chapitre, nous nous sommes penchés sur la position dans l'espace économique des plantes de trois traits physiologiques souterrains (la rhizodéposition, la respiration des racines et la colonisation par les champignons mycorhiziens), et comment ceux-ci affectent les communautés microbiennes. Ces traits se positionnaient de façon cohérente : une plus forte respiration racinaire chez les espèces acquisitives, une plus forte mycorhization chez les espèces délégatrices et une plus forte rhizodéposition chez les légumineuses, qui sont à la fois plutôt acquisitives et délégatrices. Nous avons démontré que tous les groupes microbiens étaient dépendants des photosynthétats récents, mais que la biomasse et l'allocation de ces photosynthétats n'étaient pas affectés de la même façon par les stratégies économiques des plantes.

Dans le deuxième chapitre, une approche énergétique des réseaux trophiques nous a permis de montrer que la voie énergétique basée sur les racines vivantes s'additionnait à celle basée sur les détritus, alimentant des flux plus importants jusqu'aux niveaux trophiques les plus élevés dans les traitements avec des plantes et de la litière. Nous avons aussi démontré que les espèces acquisitives tendaient à alimenter des flux plus importants.

Dans le troisième chapitre, nous avons évalué comment la stratégie économique des plantes affecte l'assimilation d'azote issu du recyclage de la litière par les végétaux et les microbes (c.a.d. la répartition de cet azote dans différents compartiments). La qualité de la litière (proportion de lignine et proportion de phosphore) était un facteur explicatif déterminant de la proportion d'azote issu de la litière retrouvé à la fois dans les microbes et les plantes. Une croissance plus rapide était aussi associée à une plus forte récupération de l'azote issu de la litière dans les plantes. Nous avons aussi souligné l'importance de la bactérivorie comme facteur explicatif de la répartition de l'azote issu de la litière entre les compartiments, bien que celle-ci ne soit pas directement impactée par la stratégie économique des plantes.

Pour conclure, nous avons identifié qu'une meilleure caractérisation des interactions biotiques était l'un des prochains défis pour l'écologie basée sur les traits souterrains. Une meilleure compréhension des préférences microbiennes pour la litière, la matière organique du sol et la rhizodéposition sera aussi déterminante pour faire le lien entre les modélisations des réseaux trophiques basées sur les flux d'énergie et le fonctionnement des écosystèmes comme le recyclage de l'azote issu de la décomposition de la litière.

Mots-clés : stratégie économique des plantes, traits fonctionnels, flux d'énergie, marquage isotopique, ^{13}C, ^{15}N

Soil biological components have been gaining renewed attention in the past years. Trophic interactions between these components support various ecosystems functions, such as biogeochemical cycles. In this manuscript, we explore how the primary producers' resource acquisition strategy impacts the quality and quantity of two basal resources: litter and rhizodeposits (Chapter 1); then we partitioned their relative importance for soil food webs (Chapter 2) and evaluated their impact on litter-derived N recycling (Chapter 3). We used the plant economics space framework to describe plant acquisition strategy, which includes two independent gradients: (i) the fast/slow gradient, opposing fast-growing metabolically efficient acquisitive species to slow-growing conservative species with longer lifespan and (ii) the exploration gradient, opposing "do-it-yourself" species with morphologically efficient root systems to "outsourcing" species relying on mycorrhizal associations. We set up a common garden experiment including 15 grassland species with contrasted strategies, crossing living plant presence and litter addition. Stable isotope labelling was used to follow the fate of carbon from rhizodeposition and nitrogen from litter decomposition in various compartments (plants, soil, microbial and faunal communities).

More specifically, in the first chapter we investigated the position of three belowground physiological traits (rhizodeposition, root respiration and AMF colonization) in the plant economics space, and how it affects microbial communities. We found that belowground physiological traits fitted logically in the plant economics space: higher root respiration for acquisitive species, higher degree of mycorrhizal colonisation for outsourcing species, and higher rhizodeposition for legumes, who are both acquisitive and outsourcing. We found that all microbial groups were dependant on recent photosynthates, but that biomass and recent photosynthates allocation were differently affected by plant economic strategies.

In the second chapter, we used a soil food web energetics approach to show that the living root-based channel adds up with the detritus channel, supporting higher fluxes up to higher trophic levels in treatment with plant and litter addition. We also demonstrated that acquisitive species tended to support higher fluxes.

In the third chapter, we delved into plant's economic strategy impact on plant and microbial uptake of nitrogen from litter decomposition (i.e. litter-derived N recovery patterns), and microbial activity. We found that high litter quality (low lignin and high phosphorus content) was determinant for high recovery in both plant and microbial compartments. Higher plant growth was also associated with higher litter-derived recovery in shoot and root systems. We also highlighted that bacterivory was a strong predictor of litter-derived N recovery patterns.

Overall, we underlined that better characterisation of biotic interactions is one of the most exciting challenges in belowground trait ecology, and that better understanding of microbial groups' preferences for litter, soil organic matter or rhizodeposition is determinant for linking soil food web modelling to ecosystem functioning like litter-derived N recycling.

Keywords: plant economic strategy, functional traits, energy fluxes, isotopic labelling ^{13}C, ^{15}N