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Plant N economics and the extended phenotype: Integrating the functional traits of plants and associated soil biota into plant-plant interactions

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Abstract

- The nitrogen (N) economics of plants are generally described in terms of functional traits and how these affect N availability in a given environment. However, recent studies have shown that plant symbionts play a crucial role in plant N economics. A plant together with its symbiont can be considered as a meta-organism, the holobiont. Plant-associated symbionts are shaped by the plant, thereby extending the plant's phenotype. Decomposers also play an important role in plant N economics yet are usually not included in the plant holobiont.
- In this review, we show the important roles that both symbionts and decomposers play in plant N economics. We focus on how plants respond to fluctuating N availability in a complex interaction network, which includes the plant's strategies and its interactions and feedback loops with the soil biota and with neighbouring plants, through competition for N by exploitation and interference.
- Synthesis: Plant N economics and the outcome of plant-plant interactions in a community cannot be fully described solely through the functional traits of plant individuals. Properties emerging from the interaction network bring new insights into plant N economics. Further research is now needed to gain a deeper understanding of plant N economics and resource economics in plant communities by integrating a broader extended plant phenotype.

Introduction

Nitrogen (N) is an essential resource that plays a key role in plant metabolism through enzyme activities and plant growth. Plant productivity is largely limited by N availability in many terrestrial ecosystems (Du et al., 2020). To mitigate this limitation, plant individuals can use N storage, internal N recycling and N exchanges with the environment. These uses define the plant's N economy, mirroring market economy theory (Bloom et al., 1985). Plants respond to fluctuations in resource acquisition and utilisation to optimise their fitness, *i.e.* their reproduction, growth and survival performance (Semenova & Maarel, 2000; Violle et al., 2007). Plant economics make use of various strategies for the acquisition and processing of resources, of which N is an important one (Ficken & Wright, 2019).

Plant economic strategies are usually described by a set of functional traits, namely morphological, physiological or phenological features measurable at the individual scale. They are most often classified on a spectrum ranging between two extremes: a *conservative strategy*, characterised by inherently slow growth, efficient internal recycling of resources and long-lifespan tissues (Reich, 2014), and an *acquisitive strategy*, promoting fast growth, resource acquisition and use, and biomass turnover. Plant trait values (their attributes *sensu* Violle et al., 2007) characterise plant individuals and position them on the spectrum of resource strategies between conservation and acquisition (Adler et al., 2014; Reich, 2014; Wright et al., 2004, **Figure 1**).

The N economies of individual plants are not set in stone and can accommodate to fluctuating N availability. Plant attributes can vary with environmental conditions depending on their phenotypic plasticity (Pigliucci, 2005; Sultan, 2000). Attributes can be heightened or attenuated in a given range (Arnold et al., 2019), the reaction norm, to respond to soil N availability and plant N status (Callaway et al., 2003; Lipowsky et al., 2015). Phenotypic plasticity has so far been only weakly integrated into plant N economics. Plasticity has generally been described as a momentary response of a plant to N availability. Yet changes in plant plasticity can confer substantial long-term changes in plant fitness (Gibert, 2020; Roscher et al., 2018).

Scientific advance has broadened the historical plant-centred view of plant strategies (Craine, 2007; Grime, 1973; Tilman, 1982), adding biotic traits related to plant-soil interactions (Freschet, Violle, Roumet, et al., 2018). Some plants rely on symbiotic relationships with N-fixing bacteria and mycorrhizal fungi to acquire N (**Figure 1**). A plant's abilities to build symbiotic interactions have therefore been integrated into the root trait

space (Reich, 2014; van der Heijden et al., 2015). Plants can also influence rates of decomposer activity, modifying N availability by acting on N cycling processes in the soil (Hobbie, 2015; Moreau et al., 2019).

Another important driver that modulates plant N economics and induces changes in plant phenotype is neighbouring plants. A plant and its neighbours all draw on a finite common N pool in the soil and cause fluctuations in N availability, with ensuing competition and/or facilitation among individuals. Plants can impede resource access of neighbours without modifying overall availability. This process, called interference competition, often involves the release of chemicals from a plant that act on neighbours, soil biota and seedbed properties (Holdridge et al., 2016). This action alters the N economics of both the releasing plant and its neighbours. Interference interactions that use chemicals directly impacting neighbours are described as allelopathic and represent the most common form of interference between plants. However, although interference is a growing field of research, it is not yet fully integrated into plant N economics. Plant functional traits involved in interference processes can be confounded with those involved in resource acquisition and processing, making plant N economics more complex than was previously thought (Fernandez et al., 2020; Inderjit & del Moral, 1997).

Plant N economics encompass (i) plant-plant interactions, (ii) plant-soil biota interactions and (iii) nitrogen availability, with reciprocal interdependencies. A new perspective is thus needed to gain a deeper mechanistic understanding of plant N economics. This will entail considering how these processes work together in the complex interaction network shaping plant N economics. Complexity is compounded by the fact that these interactions are bidirectional among all actors. Interaction networks can change according to their abiotic context because they can shift in nature and/or in intensity and importance according to resource availability (Pugnaire & Luque, 2001; Vernay et al., 2018b).

In this review, we focus on how plant-plant interactions (exploitation and interference) and plant-soil biota interactions all help shape plant N economics. We demonstrate that a functional trait approach is necessary but not sufficient to understand plant N economics, since feedback loops with neighbouring plants and soil biota are important drivers of plant N strategies at different scales. We first describe the different plant N strategies and how plant-plant interactions can affect them. We also show how plant phenotypes can be extended to integrate symbiotic microorganisms enhancing plant N acquisition as a substantial component of those

strategies. Secondly, we demonstrate why decomposers should also be included in the extended phenotype of plants and more generally in the individual plant N economy. Finally, we discuss the properties emerging from the complex interaction network including plant-plant and plant-soil biota interactions. We highlight the need to broaden the framework of plant N economics and consider the heterarchical effects of all processes on the plant-soil system (at all organisational levels).

I. Plant traits relative to different N strategies

A. Aboveground and belowground individual plant strategies to address fluctuating N availability

It has been largely demonstrated that at the individual scale, the resource economic spectrum is widely conserved among species worldwide, especially for leaf traits (Díaz et al., 2016; Wright et al., 2004). Plant strategies may adjust to fluctuating N availability through phenotypic plasticity (Abakumova et al., 2016; Roscher et al., 2018). This enables plants to manage N availability by altering their morphological (Freschet, Violle, Bourget, et al., 2018) and ecophysiological attributes (Vernay et al., 2018b). Specific leaf area (SLA), leaf N content (*Figure 1*, circle 1) and metabolic rates of processes such as leaf respiration and photosynthesis are higher in acquisitive species than in conservative ones, while leaf tissue density and lifespan are higher in conservative plants (*Figure 1*, Table 1). However, as N availability changes in space and time, plants must adjust their N economies to meet their N requirements.

A root economic spectrum has been proposed, analogous to the leaf economic spectrum. High specific root length (SRL), low root dry matter content (RDMC), high root N concentration (RNC) and high root respiration rate are associated with acquisitive species, whereas high RDMC and high lignin:N ratio are features found more often in conservative species (Prieto et al., 2015; Roumet et al., 2016). This pattern is closely related to N allocation and storage in the different organs. Acquisitive species can increase their abilities to forage for N by increasing their SRL (Hodge, 2010; Hodge et al., 1999; Oldroyd & Leyser, 2020), whereas the more conservative species preserve and store N in organs such as stems or taproots (Vernay et al., 2018b, *Figure 1*, arrows A and B).

The plant belowground compartment economy is more controversial than that of the aboveground compartment because root traits do not consistently validate a root economic spectrum mirroring the leaf economic spectrum (Mommer & Weemstra, 2012; Weemstra et al., 2016, 2021). The coordination of many morphological and architectural traits with the root economic spectrum remains unclear, especially for woody species (Erktan et al., 2018; Kramer-Walter et al., 2016). The fine-root system taking up resources in the soil was long viewed as a belowground counterpart of leaves (Liese et al., 2017). However, whereas the main function of leaves is photosynthesis, the fine-root system plays a key role in taking up water and a plethora of nutrients that are not all available in the same quantities. This suggests that plant N economy is not reducible to the traditional economic spectrum.

Bergmann et al. (2020) found a significant negative correlation between SRL and the root diameter and cortex fraction, all three traits being related to a distinct spectrum, independent of the root economic spectrum, and related to root tissue density and N content. This distinct spectrum accounts for a plant's ability to interact with soil biota to take up resources, whereby belowground interactions with the soil biota also shape plant N economy. This new axis, the *collaborative axis*, runs from a “*do-it-yourself*” plant strategy to an “*outsourcing*” strategy. Plants with a “*do-it-yourself*” strategy rely on their own functional traits to acquire N, and generally have a high SRL and small root diameter and cortex fraction. Conversely, plants with an “*outsourcing*” strategy rely on a strong interaction with root symbionts and show a low SRL but a high root diameter and cortex fraction. These attributes increase potential habitats for fungal symbionts, especially arbuscular mycorrhizal (AM) fungi. In the “*outsourcing*” strategy, the plant invests a large part of its C to strengthen interactions with mycorrhizal fungi, increasing their N acquisition (Bergmann et al., 2020). Considering root traits among the collaborative and economic gradients in the root trait space gives a new perspective on plant N economics. The soil biota closely associated with plants may thus be interpreted as an extended phenotype of plants, *i.e.* a plant genotype expression at a higher level than the plant population (Dawkins, 1982; Whitham et al., 2003, **Figure 1**). This extension had previously been suggested (Ehlers et al., 2020; Heath et al., 2010) and is a strong argument for broadening plant N strategies beyond the individual scale (Lekberg et al., 2018).

B. Plant community response to N availability

At the plant community scale, plant-plant interactions for resources can be considered as a biotic trigger of phenotypic plasticity. The nature of the neighbours and/or their density modify plant N nutrition by altering N availability in the soil (Bruehlheide et al., 2018; Minden & Venterink, 2019; Vernay et al., 2018b). To cope with a neighbourhood-induced change in N availability, target plants can accommodate N acquisition by improving (i) N use efficiency (NUE, biomass produced per unit of N taken up), (ii) N uptake efficiency (N uptake amount per unit of root biomass), or (iii) internal N cycling (assimilation and remobilisation) (Berendse & Aerts, 1987; Bouchet et al., 2016; Millard & Grelet, 2010). For instance, remobilisation at budburst of N stored in the tissues of deciduous species during the previous year will enhance photosynthesis early in the growing season (*e.g.* on oak species, Bazot et al., 2016; Vernay et al., 2018a). The N resorption rate, *i.e.* the percentage of N translocated from senescent tissues to living tissues before abscission, is generally higher in an N-depleted plant, a trait often associated with conservative species (**Figure 1**, arrow C) (Daufresne & Hedin, 2005). A recent global meta-analysis corroborated this claim and highlighted the importance of nutrient resource availability in resorption plasticity (Drenovsky et al., 2019). If plant species use the same N source, they may also spatially and temporally differentiate their N acquisition from the rest of the plant community to escape the influence of neighbours (**Figure 1**, arrow A and circle 4, Jia et al., 2020; Persson et al., 2003).

Similarly, plant interspecific relationships influence belowground plant strategies. Delayed or accelerated phenology, together with partial spatial segregation of plant root systems when soil depth allows it, offer means to escape from times and places of intense competition for N exploitation (Mueller et al., 2013; Schofield et al., 2018; Trinder et al., 2012). Historically, two opposite strategies have been proposed to explain root foraging behaviour: (i) root segregation, where plants keep their root system in free space where no neighbours are already settled and (ii) root overproduction, where plants deplete N resources down to a very low level to starve out potential competitors. A recent model showed that the two behaviours are

expressed concomitantly when tissue development and the dynamics of N in the soil are considered: plants overproduce roots in space not colonised by a neighbour and reduce root production in an area already colonised by a neighbour in accordance with the evolutionarily stable strategy (Cabal et al., 2020). Another strategy consists in changing N sources to escape from competition with neighbours. Trees may shift the N form they usually take up to accommodate competitive pressure. This hypothesis was supported by studies showing equal performance of trees despite a change in N source, through acclimation in surface area, length or diameter of fine roots, depending on the species (Zhou et al., 2019).

II. Root symbionts, an extended plant phenotype influencing N availability and plant N economy

A. Mycorrhizae and N₂-fixing bacteria

Root symbionts increase a plant's N acquisition ability by extending the potential pool of N available to it (Bruno et al., 2003; Gerz et al., 2018). The most widespread of these symbiotic associations are with mycorrhizal fungi taking up N from soil (**Figure 1**, circle 3, van der Heijden et al., 2015) and N₂-fixing bacteria (*Rhizobium* and *Frankia*, **Figure 1**, arrow H) fixing atmospheric N in an organic form (Carranca, 2013; Carvalho et al., 2014). These associations can promote photosynthesis and growth and contribute to an acquisitive economic strategy (Parisi et al., 2015; Simard & Durall, 2004). Mycorrhizal fungi enable a host plant to expand its N prospection area and help it compete for N with decomposer microbes (Fellbaum et al., 2012; Hodge & Fitter, 2010; S. Simard et al., 2015). Accordingly, mycorrhizal colonisation rate is considered as a biotic root trait characterising plant N strategies (Bardgett et al., 2014; Fellbaum et al., 2014; M. L. McCormack et al., 2017). Plant N strategies thus imply some processes occurring at the scale of the *holobiont*, a functional entity composed of the plant host and the associated microorganism communities (Gordon et al., 2013; Hassani et al., 2018). The concept of plant holobiont implies resource exchanges and an associated C-N exchange trade-off between the plant and its microbiome, to meet the needs of both partners and sustain the reciprocal interactions (Ke et al., 2015; Meiners et al., 2017; Pregitzer et al., 2010).

Although plant-symbiont interactions remain essential for both partners, the relationship can in some cases be viewed as reciprocal parasitism (Cahill & McNickle, 2011). Some studies have revealed “*cheater*” strategies in root symbiotic biota: microorganisms may trade a small amount of N or other nutrients for an unfairly large supply of C or other resources from the plant. This behaviour shifts the two-way interaction to the advantage of the root symbionts, at the expense of the fitness and performance of their plant host (Kiers et al., 2003). To redress this imbalance, plants can deploy a “*reward-sanction*” strategy: they supply more C to the best N symbiont suppliers and cut back supplies to the “*cheaters*” to restore equity (Fellbaum et al., 2014; Kiers et al., 2003). However, the soil symbiotic biota also have control over the symbiosis, and can supply more N to the most carbohydrate-generous host plants and still make a net profit (Fellbaum et al., 2014; Weremijewicz et al., 2016).

Overall, the regulation of the symbiosis by both partners may turn a suboptimal trait value for an individual (*e.g.* loss of C transferred by a plant to its symbionts) into an advantage at the holobiont scale, improving the potential benefit of association with a partner (Carthey et al., 2020; Friesen et al., 2011). As far as we know, cheating behaviour cannot be maintained in the long term. Instead, there are probably constant reciprocal adaptations between the plant and the symbionts until they find a satisfactory trade-off (Batstone et al., 2020). The cooperative behaviour between the plant host and its symbionts may be altered by environmental conditions, swinging temporally to the advantage of either the plant host or the symbionts before reverting to a more mutualistic relationship (Frederickson, 2013, 2017). For instance, Heath et al. (2010) showed in their study that the interactions between legumes and rhizobia changed according to partner genotypes and the availability of nitrates. These changes in the symbiotic interaction towards an optimised mutualism were observed in several generations. The nitrate response of legume-rhizobium nodulation is akin to a strongly plastic extended plant phenotype that maintains the reciprocal benefits for the legumes and rhizobacteria despite environmental variation and genetic diversity of the rhizobacteria symbionts.

B. Plant growth-promoting rhizobacteria

Plant growth-promoting rhizobacteria (PGPRs) are a growing subject of study in both natural and crop environments. They are free-living bacteria found in the soil close to a plant that can enhance plant growth through direct processes such as production of phytohormones, reduction of ethylene, and increased biotic

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resistance to pathogens. They can also promote indirect processes such as pathogen control or the stimulation of symbiosis (Antoun & Prévost, 2006; Lugtenberg & Kamilova, 2009; Van, 2007). Although PGPRs have been largely studied to improve field crop yields (Backer et al., 2018; Kumar et al., 2018; Vejan et al., 2019), the processes are also relevant for less strongly anthropised ecosystems despite some differences in the PGPR community diversity (Flores-Núñez et al., 2018). PGPRs can help plants acquire N through mechanisms very close to those involving rhizobia. For instance, *Azospirillum* can produce nodules on a plant's roots and are also able to fix atmospheric N₂ (Antoun & Prévost, 2006). More interestingly, the combination of PGPRs and symbionts can have a synergetic effect on plant growth. Studies show that the presence of PGPRs promotes root length density, increasing N foraging plant abilities and the potential sites of infection by rhizobia (Dobbelaere et al., 2003 and references therein). Similarly, PGPRs stimulate AM fungi colonisation and then N uptake by hyphae, thereby enhancing plant growth (Antoun & Prévost, 2006). The effect of PGPRs on ectomycorrhiza (EM) colonised trees is more controversial as both beneficial and adverse effects on mycorrhization have been observed (Antoun & Prévost, 2006). We do not know of any general review or metanalysis of PGPR effects on plants in natural ecosystems. These effects thus warrant more research, especially since their importance for plant N strategies could be critical.

III. Decomposers as part of the plant extended phenotype

Decomposer organisms are also important determinants of plant N economics owing to the key role they play in shaping soil properties and N cycling (Table 1). The common definition of holobiont combines plant host and associated microorganisms. Symbiotic microorganisms interact very closely with their plant hosts because they are physically coupled to them, whence a broad consensus in the scientific community to include symbionts in the plant holobiont (Simon et al., 2019; Vandenkoornhuyse et al., 2015). However, free-living microorganisms in the rhizosphere are not always included in the holobiont (Gordon et al., 2013; Vandenkoornhuyse et al., 2015). In this section, we advance some arguments for integrating decomposers into the extended phenotype of a plant and in the plant holobiont structure, as they are also engaged in close reciprocal interactions with plants (*Figure 1*).

A. Influence of biotic interactions between plants and decomposer microbes on N economy

Decomposer microbes play an important role in soil N cycling by depolymerising and metabolising litter (**Figure 1**, arrow E and circle 2.), thereby allowing the recycling of litter N back into dissolved forms (mineral or organic) available for uptake by plants (Schimel & Bennett, 2004). There has so far been a consensus that acquisitive species adapted to fertile habitats promote N mineralisation and mineral N availability to plants by producing large amounts of labile N-rich litter that decomposes quickly. Conversely, conservative species dominating infertile habitats promote N immobilisation in microbial biomass and restrict N availability to plants by producing recalcitrant N-poor litter that decomposes slowly (**Figure 1**, arrows D, E & F, Wardle et al., 2004). This paradigm has mainly focused on the early stage of litter decomposition and overlooked soil organic matter (SOM) that has undergone further processing by decomposer organisms (Hobbie, 2015). However, microbes decomposing fresh litter often experience stoichiometric imbalance because fresh litter is usually too N-poor to meet the N requirements imposed by their relatively homeostatic behaviour (Mooshammer et al., 2014). The resulting N limitation of microbial growth explains why decomposer microbes typically retain most of the organic N from litter rather than mineralising it early during decomposition (Mooshammer et al., 2014). When the stoichiometric imbalance is too high, decomposer microbes can also immobilise mineral N from the surrounding soil to meet their N demand (Hobbie et al., 2006; Parton et al., 2007). Consequently, the decomposition of fresh litter and particulate organic matter (POM) lead to a minor increase or even a decrease in N availability to plants (Fornara et al., 2011; Whalen et al., 2000). This could preclude short-term positive feedback to soil N availability operating through litter decomposition (Knops et al., 2002). Nevertheless, organic matter becomes progressively more N-enriched over the course of decomposition because part of its C is lost by microbial respiration (Mooshammer et al., 2014). Some of the remaining organic matter is then used by microbial decomposers for their growth, and when these die, the accumulating plant and microbial residues could form N-rich SOM (Angst et al., 2019; Schmidt et al., 2011). When the reactivity of soil minerals is high enough to form chemical associations with organic matter, SOM formation can also eventually lead to large amounts of organic N being stored as mineral-associated organic matter (MAOM) in soil mineral layers (Cotrufo et al., 2019; Lehmann & Kleber, 2015). Although MAOM has historically been considered a relatively passive reservoir of soil organic N,

recent conceptual progress based on a growing body of empirical evidence now highlights the dynamic nature of MAOM as a large reservoir of SOM enriched in N that can be actively mined by microbes and roots (Daly et al., 2021; Jilling et al., 2018). The decomposition of SOM found in humified organic layers or as MAOM in mineral layers has been found to promote N mineralisation (Whalen et al. 2000, Fornara et al. 2011, Mooshammer et al., 2014b), thus representing a major source of N available to plants (**Figure 1**, arrow F).

There is now a large body of evidence that plants can actively accelerate the decomposition of SOM through their living root activities, a phenomenon called the “rhizosphere priming effect” (Dijkstra et al., 2020). Plant roots release organic compounds such as exudates, sloughed cells and mucilage to soil by rhizodeposition, which represents around 10% of plant C input to soil (Pausch & Kuzyakov, 2018). Rhizodeposition of soluble and energy-rich compounds such as carbohydrates can stimulate rhizosphere microbes and their production of exoenzymes catabolising SOM decomposition (Zhu et al., 2014). Rhizodeposition of organic acids acting as ligands can also increase the accessibility of MAOM for microbial decomposers by disrupting organo-mineral associations (Clarholm et al., 2015; Keiluweit et al., 2015). Finally, rhizodeposition of labile C coupled to root N uptake can induce N limitation of microbial growth in the rhizosphere, thus causing microbes to use rhizodeposition to mine N-rich SOM to meet their demand (Craine, 2007; Fontaine et al., 2011; Henneron, Kardol, et al., 2020). Although the stimulation of microbial growth in the rhizosphere can lead to strong N immobilisation in the short term, plant roots are stronger competitors than microbes for N acquisition in the long run because of their longer lifespans and the release of microbial N by faunal grazing (Kuzyakov & Xu, 2013; Trap et al., 2015). The rhizosphere priming effect has been shown to be associated with enhanced gross rates of soil N mineralisation and faster microbial biomass turnover, thereby greatly improving N availability for plant uptake (Dijkstra et al., 2009; Henneron, Kardol, et al., 2020).

The positive feedback among plants, soil properties and N cycling differs markedly between plant economic strategies (Table 1, Hobbie, 2015). Acquisitive plant species are often found in fertile soils with moderate acidity and abundant reactive minerals (Kramer-Walter et al., 2016; Maire et al., 2015; Ordoñez et al., 2009), and their production of large amounts of labile N-rich litter can therefore lead to the formation of N-rich SOM stored as MAOM in mineral layers (Angst et al., 2019; Cotrufo et al., 2019; Craig et al., 2018). This can promote N mineralisation and allow marked nitrification, thereby further increasing N availability, given the

higher mobility of NO_3^- relative to NH_4^+ (Fornara et al., 2011; Legay et al., 2020; Orwin et al., 2010).

Acquisitive plant species are associated with higher rates of rhizodeposition (Guyonnet et al., 2018; Henneron, Cros, et al., 2020; Sun et al., 2021; Williams et al., 2021), thus accelerating soil N cycling through rhizosphere priming of SOM decomposition (Han et al., 2020; Henneron, Kardol, et al., 2020). Acquisitive plant species can thus promote soil N mineralisation by rhizosphere priming and regulate the balance between soil organic N formation and mineralisation depending on their demand (Fontaine et al., 2011; Henneron, Kardol, et al., 2020). They thereby improve their nutrition and sustain their fast growth in fertile habitats while also promoting N retention in microbial biomass during plant resting periods (Abalos et al., 2018; Cantarel et al., 2015; de Vries & Bardgett, 2016).

Unlike acquisitive plants, conservative plant species are mostly found in infertile soils with marked acidity and sometimes a low abundance of reactive minerals, and their production of recalcitrant N-poor litter decomposing slowly leads to the formation of relatively N-poor SOM in organic layers or as POM in mineral layers (Cotrufo et al., 2019; Ponge, 2013). This leads to strong N retention by decomposer microbes because it promotes low mineralisation of litter N and high immobilisation of soil mineral N, thereby keeping N availability to plants at low levels dominated by dissolved organic forms of N (Högberg, 2007; Northup et al., 1998; Wardle et al., 2012). Some plant species can limit short-term N losses due to leaching or denitrification by controlling biological inhibition of nitrification or denitrification in their rhizosphere (Bardon et al., 2014, 2018; Lata et al., 2004; Subbarao et al., 2009). Another important mechanism by which conservative woody plant species inhibit litter decomposition and soil N mineralisation is through their high production of secondary metabolites such as polyphenols (Hättenschwiler & Vitousek, 2000; Kraus et al., 2003). Condensed tannins produced by woody plant species are known to form complexes with proteins that are then recalcitrant to decomposition. Given the high mobility of mineral N, the sequestration of organic N in soil by conservative plant species could help prevent long-term ecosystem N losses due to leaching or denitrification in infertile habitats (de Vries et al. 2012, Grigulis et al. 2013, Arnoldi et al., 2020; Northup et al., 1998). This also promotes a slow but dominant plant uptake of organic N, bypassing the mineralisation by microbial decomposers (Näsholm et al., 2009; Schimel & Bennett, 2004). Conservative plant species are also able to

enhance SOM decomposition by rhizosphere priming, but this promotes availability of N to plants in organic rather than mineral form (Adameczyk et al., 2019).

B. Mycorrhizal influence on decomposition

Different groups of mycorrhizal fungi are associated with contrasting plant economic strategies and ecosystem N dynamics (Averill et al., 2019; Phillips et al., 2013; Tedersoo & Bahram, 2019) (*Figure 1*, circle 3).

Acquisitive plant species are mostly associated with AM fungi that have limited decomposition abilities. AM tree species are usually associated with faster SOM decomposition (Taylor et al., 2016; Wurzbürger & Brookshire, 2017), and AM fungi have been found to help acquisitive plant species accelerate SOM decomposition through rhizosphere priming by enhancing rhizodeposition supply to soil (Hodge & Fitter, 2010; Paterson et al., 2016) and to enhance plant N acquisition of mineralised N from SOM decomposition (Hodge & Fitter, 2010). Conversely, conservative plant species are mostly associated with ericoid mycorrhizal (ERM) or ectomycorrhizal (ECM) fungi that have strong decomposition abilities. ERM, and to a lesser extent ECM fungi, have been found to enhance the ability of conservative plant species to mobilise N sequestered in their litter as tannin-protein complexes (Wurzbürger & Hendrick, 2009). For example, it has been shown that the presence of poorly decomposable leaf litter and ECM fungi together improve N acquisition and growth in beech tree seedlings through decreasing N immobilisation by free-living microbial decomposers (Trap et al., 2017). ERM and ECM fungi are thus key drivers of organic N nutrition for conservative species, helping them compete for N against decomposer microbes.

C. Consequences of decomposer and mycorrhizal activities associated with N cycling for plant-plant interactions

The influence of plant species on soil N cycling can have strong effects on interspecific competition for N in plant communities. For example, the dominance of conservative ericoid plant species in early successional stages of heathlands has been attributed to the production of poorly decomposable litter, excluding more acquisitive grass species by maintaining low soil mineral N availability (Berendse, 1998). After atmospheric N deposition has increased soil N availability, grasses gradually become dominant as the accumulation of N-rich SOM formed from their litter leads to an increase in soil N mineralisation, thus further enhancing long-

term mineral N availability. This deprives the ericoid species of their relative advantage owing to organic N nutrition by ERM fungi and increases the competitiveness of the grasses relying on soil mineral N. Similarly, high production of condensed tannins by ericaceous shrubs promoting the sequestration of soil N as tannin-protein complexes has been suggested to improve the competitive ability of ericaceous shrubs relative to ECM tree seedlings by favouring organic N uptake by their ERM fungi during forest regeneration in boreal forests (Joanisse et al., 2009).

A given plant species can also regulate its influence on soil N cycling in response to the presence of neighbours and their identities by phenotypic plasticity. For example, following treefall disturbances and tree canopy opening in temperate forests, mature oak trees have been found to produce leaf litter poorer in nutrients and richer in condensed tannins, slowing down its decomposition and increasing N immobilisation (Henneron et al., 2017). This litter N sequestered in tannin-protein complexes can then be mobilised by oak seedlings through their ECM partners, while it will be unavailable to AM understory plants. This could therefore represent an adaptive strategy of oak trees, which by monopolising the N contained in their litter to save their pre-empted N pool from capture by outcompeting understory plants, can be more competitive in treefall gaps during forest regeneration.

Overall, decomposers are strongly influenced by plant strategies, and their activities in turn affect plant fitness in a given environment by modulating N availability (Henneron, Kardol, et al., 2020; Moreau et al., 2019; Trap et al., 2017). We therefore argue that decomposers should be included in the extended plant phenotype together with the symbiotic soil biota, and that decomposers thus belong to the plant holobiont.

IV. Plant N economics in a complex heterarchical network

Changes in plant performance and attributes will trigger modifications in plant-soil biota interactions (Zhalnina et al., 2018), in turn modifying holobiont N economics. Conversely, plant-soil biota interactions may induce changes in a plant's attributes. The resulting feedback loops can change the plant and soil community properties and produce effects at ecosystem scale by modifying N fluxes and plant community structure (Cantarel et al., 2015; Legay et al., 2016; Png et al., 2019). Plant N economics thus operate in a heterarchical network. A heterarchical network is an organisation in which all the actors of the system may

interact with each other. It differs from a hierarchical network, which allows only vertical interactions between an organisation level n and its next higher level ($n + 1$). It also differs from a network with no organisation levels (Cumming, 2016). In a heterarchical network, for a given scale (individual plant, holobiont, soil biota, plant community), top-down, bottom-up and peer-to-peer interactions all occur, producing effects at different scales. The concept of the heterarchical network thus seems well-suited to plant N economics. The earlier hierarchical “Russian dolls” approach (plants influence soil biota to acquire N, in turn changing their performance and impacting the community properties, and finally affecting ecosystem functioning) did not really embed plant-plant and plant-soil biota interactions as a strong driver of plant N economics. Heterarchical interaction, though making plant N economics much more complex, opens new ecological perspectives. Because plant N economics do not depend merely on an individual plant’s trait but also on its extended phenotype, with its own response to N availability and biotic interactions, the plant at the individual and holobiont scales must exchange numerous signals between all components of the heterarchical system.

A. Impact of multiple cues from neighbours on rhizosphere community and on plant-soil biota interactions

Effects of interference on plant N economics have been less thoroughly explored than resource interactions, even though interference can have a marked impact on a plant’s ability to acquire and use N. Interference involves signalling pathways connecting emitter and receiver plants or soil microorganisms (*Figure 1*, circle 3). An increasing number of studies have identified key chemical cues with a signalling function, mainly in litter and rhizodeposits released by plants (Pierik et al., 2013, van Dam et al., 2016), such as organic acids, sugars, mucilage and secondary metabolites, or foliar substances. Exudates impact the recruitment of symbionts and decomposers, thereby indirectly shaping resource availability conditions (Boeddinghaus et al., 2019; Guyonnet et al., 2018; Lombardi et al., 2018). Through root exudation, plant-plant interactions can be exacerbated. In a heterospecific context, a ^{15}N labelling study recently demonstrated that purple moor grass (*Molinia caerulea*), a strongly monopolistic grass, could induce higher N-rhizodeposition from an oak seedling neighbour and take up this new N source for its own use in addition to soil N (Fernandez et al.,

2020). In the case of *Molinia versus Quercus* interactions, the acquisitive strategy of the grass allows a quick capture of N exudates, thereby precluding its re-uptake by oak seedlings (Vernay et al., 2016).

Nodulation or mycorrhizal colonisation can be reduced after the release of cues from a focal plant, increasing its competitiveness *via* a decreased N symbiont supply to its neighbour. This mechanism is well documented for *Alliaria sp.*, which releases allelopathic substances disturbing the mycorrhization of neighbours (Callaway et al., 2008). Conversely, root-associated soil biota can inactivate a plant neighbour's chemical cues in the soil and reduce the competitiveness of that neighbour for N acquisition (Cipollini et al., 2012, and references therein). As an interface between plant and soil, symbionts are important players for improving plant N acquisition, but they also represent a target in plant-plant interactions to degrade a neighbour's competitiveness.

As exudate composition changes during a plant's life and in response to environmental fluctuations, exudates also induce a change in the root symbiont community, modifying the holobiont properties related to N economics (Zhalnina et al., 2018). The symbiosis is changed according to the plant's requirement regardless of N availability. Chemical cues then regulate plant-plant and plant-soil interactions and trigger changes in competitiveness or cooperativeness in the plant community (Sasse et al., 2018; Wang et al., 2021). (**Figure 1**, arrow G, Wang et al., 2021). Released substances such as strigolactones may favour colonisation by mycorrhiza (Kessler & Kalske, 2018), while flavonoids improve rhizobia or PGPR recruitments (Hassan & Mathesius, 2012). Concomitantly, PGPRs and rhizobacteria, belonging to the plant extended phenotype (*e.g.*, *Azospirillum*, *Ps. Putida*, *A. brasilense*) are known to release some phytohormones such as indole-3 acetic acid (Richardson et al., 2009; Spaepen et al., 2007) or ethylene (Richardson et al., 2009). These substances indirectly increase plant N uptake, promoting root elongation, higher SRL, root branching and root hair proliferation. This helps extend the prospection zone.

The control by plants of the release of chemical cues and their potential multiple effects in the surrounding environment needs further research (Pierik et al., 2013). How receiver plants or soil biota perceive a secreted chemical cue is still uncertain, since the effect of the cue on the receiver depends on the plant legacy and adaptation to neighbours (Callaway et al., 2008). Several studies have demonstrated the importance of recognition to form the holobiont and to attract specific soil biota in the rhizosphere (Badri & Vivanco, 2009;

Brencic & Winans, 2005; Reinhold-Hurek et al., 2015). However, quantifying this exudation flux and identifying its molecular composition *in vivo* remains a challenge, although recent methodological progress is encouraging (Buckley et al., 2019; Oburger & Jones, 2018). Improving the methodology would greatly help in elucidating the mechanisms of interference processes and the impact of N availability on exudation rates (Kaštovská et al., 2017).

B. Are plant N strategies a “family business”?

In a conspecific interaction context, a neighbour’s response depends on kinship (*i.e.* the degree of relatedness of individuals), which implies kin recognition independently of N availability (Dudley & File, 2007). A study suggested a change in *D. cespitosa* trait values that increased its foraging abilities in the presence of non-kin individuals (Semchenko et al., 2014). This change could potentially increase N availability for the kin by a decrease in competition by exploitation and reduce it for heterospecific neighbours. The kin recognition processes lead to a change in plant behaviour to adapt plant N economics. The study found that root exudates contained specific information about kinship, supporting the crucial signalling role of compounds released by a plant. The differential plant response depending on the relatedness of neighbours can be interpreted in either of two ways: (i) the kin limit their own competitive pressure for N resources to increase N availability for their relatives or (ii) the kin increase their competitive abilities when they encounter unrelated or heterospecific individuals. Either way, the altered plant N economics have effects at plant population and community levels, potentially fostering N availability for conspecific individuals to the detriment of heterospecific individuals. Kin recognition shows that resource exploitation and interference co-occur in a plant community, involving interactions at different scales in the heterarchical system.

C. Soil biota, a vector of cues

Chemical cues can be conveyed through the mycorrhizal network, as can allelopathic substances (**Figure 1**, circle 3) (Canarini et al., 2019). Compounds inducing positive or negative responses in the receiver can be translocated through different pathways, at either the individual or the holobiont scale. The initial net reciprocal benefits of the symbiotic interaction between a plant and its mycorrhizal fungi may shift to a net negative effect, at least on the plant. Besides N, mycorrhizal fungi may convey allelopathic compounds,

whose negative effect may undo the benefit of the N supply (Barto et al., 2011; Gorzelak et al., 2015). The mycorrhizal network can be used by plants to transfer N compounds to a neighbour (He et al., 2019; Simard, 2018), which may be beneficial at least for one plant partner in the network (**Figure 1**, circle 3). Teste et al. (2015) showed that a plant can transfer up to 4% of its N to another plant through the mycorrhizal network. They suggest that a source-sink relationship between donor and receiver drives the transfer, a growing receiver increasing the N amount transferred from the donor to meet its requirements. This would mean that the plant's strategy impacts N flux: acquisitive plants, with high N demand, would then be stronger sinks than conservative ones. Fernandez et al. (2020) showed the involvement of hyphae in the transfer of N between oak seedlings and *Molinia*. This prompted the authors to suggest that *Molinia* uses the mycorrhizal network to induce a high N transfer from oak for its own benefit, but this hypothesis needs more supporting evidence. Although N mycorrhizal transfer was first demonstrated with legumes as donor, it also occurs among non-legume plants (Fernandez et al., 2020; Teste et al., 2015). This process can substantially influence plant-plant interactions and plant N economics and emphasises the need for more research to determine the drivers of these transfers and their consequences at holobiont scale.

V. Perspectives

The foregoing sections highlight the complex interaction network in which plants are engaged. For plant N economics, we show that this network depends on several actors at different organisational levels. At the individual scale, plant N uptake and processing is influenced by the plant strategies (*i.e.* their trait attributes) together with their symbionts and associated decomposers, considered as part of their extended phenotype. The holobiont scale at the uppermost level has its own properties linked to N economics, which may benefit the plants and/or their associated soil biota. At different scales, plants interact with other neighbouring plants. The heterarchical interaction network increases the complexity of plant N economics and reveals some emerging properties influencing N cycle and plant-plant interactions, ultimately leading to plant population and community changes.

Environmental modulation of holobiont properties and N availability can induce changes in the intensity and importance of biotic interactions among plants. Biotic interaction intensity refers here to the absolute effect of

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the presence of a neighbour on a focal plant and the relative importance of these biotic interactions compared with environmental factors on the focal plant's performance (Brooker et al., 2005; Corcket et al., 2003; Weigelt & Jolliffe, 2003). We know that at an individual scale, plant interactions change along an environmental gradient as a result of different strategies and tolerance to abiotic stress (Bertness & Callaway, 1994; Fajardo & McIntire, 2011; Pugnaire & Luque, 2001). However, while the symbiont and decomposers exert strong interactions with their host, they also respond to environmental fluctuations. The intensity and importance of plant-plant interactions may then be altered as previous studies have shown, but the mechanisms will involve not only the plant's trait plasticity but also the response of the whole holobiont to the environmental changes. Holistically, it would thus be more relevant to investigate plant holobiont-plant holobiont interactions to describe plant N economics.

Taking the soil biota associated with plants as an extended plant phenotype and including them in the plant N economics lends more flexibility to the interpretation of N dynamics in a plant community. N economics depend on more complex interactions than mere resource acquisition strategies. In their perspective, Franklin et al. (2020) claimed that model predictions on vegetation dynamics might diverge because of "*contrasting or incomplete representations of nitrogen (N) uptake, responses to soil moisture and mortality*". We recognise that in a modelling perspective, increasing complexity will necessarily lead to increased uncertainty. However, the mechanistic approach at different scales can provide some explanations for the variability observed in model estimates of N and community dynamics. Although we agree with Franklin et al. (2020), we still emphasise the key role of the heterarchical network of biotic interactions in a plant community. However, this raises some unanswered ecological/ecophysiological questions. What are the processes that trigger and modulate the release of interfering cues in the soil? What are the targets of these cues? Can interference mechanisms change the nature and the intensity of N exploitation interactions? From the perspective of biotic interactions, it is unclear to what extent soil biota influence plant behaviour in response to N availability. A subsidiary question may then arise. How intense and important are the reciprocal influences between plants and associated soil biota? How do their intensity and importance vary according to biotic and abiotic factors? Focusing on feedback plant response to plant-plant interactions, it would also be useful to know whether plant litter composition is a plastic trait that varies in response to plant-plant interactions, influencing SOM decomposition. Finally, what emergent

properties characterise the holobiont? To what extent do emergent properties of the holobiont influence its environment?

As pointed out in a recent review, plant community functioning, in our case focused on N economics, should be characterised in terms of the processes linking each node in the system. Merely understanding each actor in the plant community network is not sufficient to describe the community, because interactions and their associated ecophysiological processes need to be considered (Perronne et al., 2017). The effects of environmental changes and biotic interactions on actors in the network will then feed back over the network. The dynamic interactions in this heterarchical network and the induced feedback loops will lead to self-organisation, *i.e.* a dynamic reshaping of the internal structure of the network. The network will tend to maximise network complexity to maximise network stability (Levin, 2005; Parrott, 2010). Stabilisation will result from stronger or more numerous interactions between each component of the plant community; the network is then more robust when threatened with disturbances that could impair some of the interactions. We therefore argue that plant strategies result in complex plastic behaviour, integrating the effects and responses of all the network participants at different scales. Considering the dynamism of interactions in a heterarchical system will help gain a deeper understanding of plant N economics, with possible applications such as in agroecological or conservation management (Abalos et al., 2019; Zirbel et al., 2017).

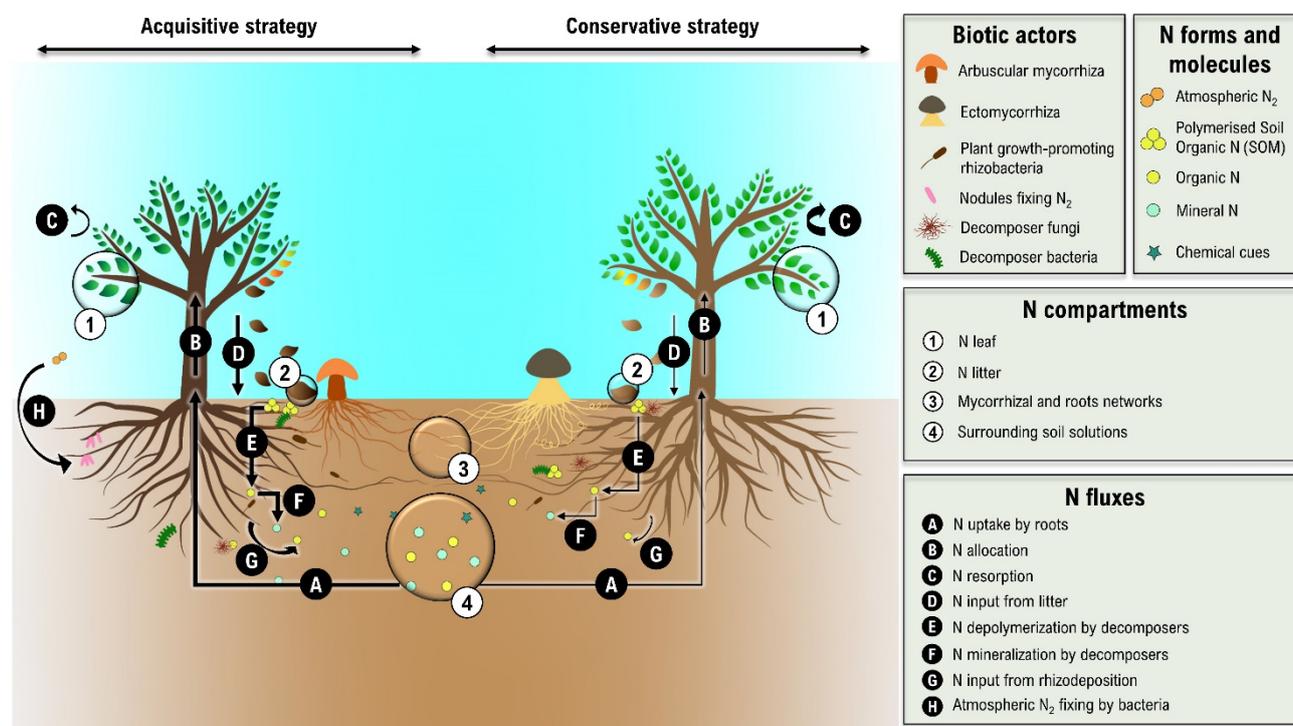
Conclusion

In this review, we reconsider N economic strategies. Historically, plant strategies were most often described in terms of their functional traits for a given soil N fertility. Symbiotic partners were later added as a critical part of these strategies. Here we further broaden their scope by considering free decomposers influenced by the plants. Extending the plant phenotype allows a more holistic characterisation of plant N economy because the holobiont encompasses the complex network of biotic interactions influencing plant N strategies. This prompts us to argue for a more integrative view of plant N strategies. N economy is not an individual feature but the dynamic net outcome of plant traits, neighbour influence, and plant-soil biota interactions according to N availability. The complex feedback loops between these three compartments need to be integrated to gain a

mechanistic understanding of how plants manage N resources in plant communities. Considering the close association of a plant with its symbionts and decomposers as an extended plant phenotype would thus place plant N economics in a new light. It is now time to consider plant N economics in a complex system perspective to better understand how local abiotic and biotic conditions shape plant N economics. Alongside resource exploitation processes, interference mechanisms and signalling chemical compounds make an important contribution to the interaction network, and so should not be neglected when considering plant N economics. Further research should focus on the relative contributions of interference *versus* resource exploitation as competition mechanisms to help explain plant community dynamics. This approach can produce different outcomes in terms of plant abundance, composition, and plant functional group distribution from overall predictions based on plant functional traits alone (Bruehlheide et al., 2018).

Figure captions

Figure 1. Overall scheme of plant-plant and plant-soil interactions driving plant N economics. Acquisitive (left) and conservative (right) plants are represented with their different impacts on the N cycle. The size of the arrows represents the relative weights of the mechanisms between the two contrasting strategies. Arrows show the different pathways and directions of N and chemical cues exchanged between plants.



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	Plant species with an acquisitive economic strategy	Plant species with a conservative economic strategy	Empirical evidence
Plant traits			
Plant growth rate	High	Low	Kramer-Walter et al., 2016; Lambers & Poorter, 1992; Orwin et al., 2010
Leaf and root lifespan	Low	High	Craine et al., 2002; L. M. McCormack et al., 2012; Tjoelker et al., 2005; Wright et al., 2004
Leaf and root respiration rate	High	Low	Craine et al., 2002; Tjoelker et al., 2005; Wright et al., 2004
Leaf photosynthetic rate	High	Low	Tjoelker et al., 2005; Wright et al., 2004
Root nitrogen uptake rate	High	Low	Legay et al., 2020; Maire et al., 2009
Root exudation rate	High	Low	Guyonnet et al., 2018; Henneron, Cros, et al., 2020; Sun et al., 2021; Williams et al., 2021
Leaf and root nitrogen resorption efficiency	Low	High	Deng et al., 2018; Vergutz et al., 2012
Leaf and root decomposability	High	Low	Freschet et al., 2012; Hobbie et al., 2006; Northup et al., 1998
Dominant mycorrhizal types	Arbuscular mycorrhizae	Ericoid or Ectomycorrhiza	Averill et al., 2019; Craig et al., 2018; Phillips et al., 2013
Soil properties			
Dominant humus form	Mull	Moder or Mor	Reich et al., 2005; Wardle et al., 2012
Forest floor turnover rate	High	Low	Hobbie et al., 2006; Reich et al., 2005
Soil organic matter C:N ratio	Low	High	Craig et al., 2018; Högberg, 2007; Kramer-Walter et al., 2016; Ordoñez et al., 2009; Reich et al., 2005
Dominant soil organic matter fraction	Mineral-associated organic matter	Particulate organic matter	Angst et al., 2019; Cotrufo et al., 2019; Craig et al., 2018
Rhizosphere priming effect on soil organic matter	High	Low	Han et al., 2020; Henneron, Cros, et al., 2020
Acidity	Low	High	Högberg, 2007; Kramer-Walter et al., 2016; Maire et al., 2015; Reich et al., 2005
Base cation saturation	High	Low	Reich et al., 2005
Dominant soil food web energy channel	Bacterial-based energy channel	Fungal-based energy channel	Högberg, 2007; Kramer-Walter et al., 2016; Maire et al., 2015; Reich et al., 2005
Dominant soil fauna	Earthworms	Enchytraeid and microarthropods	Reich et al., 2005
Decomposer abilities of mycorrhizal fungi	Low	High	Phillips et al., 2013; Wurzburger & Hendrick, 2009
Soil nitrogen cycling			

Dominant form of dissolved nitrogen	$\text{NO}_3^- / \text{NH}_4^+$	$\text{NH}_4^+ / \text{amino acid}$	Craine et al., 2002; Legay et al., 2020; Northup et al., 1998; Phillips et al., 2013; Wardle et al., 2012
Gross protein depolymerisation rate	High?	Low?	Little evidence, but see Mooshammer et al., 2012
Gross nitrogen mineralisation rate	High	Low	Fornara et al., 2011; Henneron et al., 2020; Högberg, 2007; Mooshammer et al., 2014
Nitrogen immobilisation by microbial biomass	High on short-term but low on long-term	Low on short-term but high on long-term	de Vries & Bardgett, 2016; Grigulis et al., 2013; Henneron et al., 2020; Vries et al., 2012
Net nitrogen mineralisation rate	High net mineralisation to low net immobilisation	Low net mineralization to high net immobilisation	Craine et al., 2002; Deng et al., 2018; Hobbie et al., 2006; Ordoñez et al., 2009; Orwin et al., 2010
Nitrification rate	High	Low	Cantarel et al., 2015; Laughlin, 2011; Orwin et al., 2010; Phillips et al., 2013
Denitrification rate	Low on short-term but high on long-term	High on short-term but low on long-term	Abalos et al., 2018; Cantarel et al., 2015; Grigulis et al., 2013
N leaching	Low on short-term but high on long-term	High on short-term but low on long-term	de Vries & Bardgett, 2016; Grigulis et al., 2013; Vries et al., 2012
