



## Tansley review

# Symbiont plasticity as a driver of plant success

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## Summary

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**Key words:** flexible mutualism, geographic occupancy, landscape structure, mycorrhiza, nitrogen fixers, pathogens, plant–soil interactions, species abundance.

We discuss which plant species are likely to become winners, that is achieve the highest global abundance, in changing landscapes, and whether plant-associated microbes play a determining role. Reduction and fragmentation of natural habitats in historic landscapes have led to the emergence of patchy, hybrid landscapes, and novel landscapes where anthropogenic ecosystems prevail. In patchy landscapes, species with broad niches are favoured. Plasticity in the degree of association with symbiotic microbes may contribute to broader plant niches and optimization of symbiosis costs and benefits, by downregulating symbiosis when it is unnecessary and upregulating it when it is beneficial. Plasticity can also be expressed as the switch from one type of mutualism to another, for example from nutritive to defensive mutualism with increasing soil fertility and the associated increase in parasite load. Upon dispersal, wide mutualistic partner receptivity is another facet of symbiont plasticity that becomes beneficial, because plants are not limited by the availability of specialist partners when arriving at new locations. Thus, under conditions of global change, symbiont plasticity allows plants to optimize the activity of mutualistic relationships, potentially allowing them to become winners by maximizing geographic occupancy and local abundance.

## I. Introduction

Overall, some species perform better than others, and we can rank species on this basis. Ever since Darwin (1859) asked, ‘Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?’, the topic has captured the attention of naturalists and scientists alike. Plant ecology provides information about the traits and life history strategies that contribute to plant success in particular conditions along stress and disturbance gradients (Grime, 2001; Westoby *et al.*, 2002; Funk *et al.*, 2017). However, increasing human impact at local and global scales is creating environmental conditions that are unprecedented in biogeographic history. McKinney & Lockwood (1999) suggested that many species are currently declining because of human activities (‘losers’) and are being replaced by a smaller number of expanding species that thrive in human-altered environments (‘winners’). Therefore, it would perhaps pay to reformulate Darwin’s question: Why is one species successful in human-altered conditions while another is not? This question still awaits an answer.

In our search for an answer, we may start with Darwin’s description of successful species – those that range widely and are numerous. We propose combining these components and defining winners as species that exhibit the highest product of local abundance and geographic occupancy (Box 1). This approach corresponds to Preston’s (1948) concept of ‘global abundance’, defined as the total number (abundance) of living individuals of a given species. Which of the two components is relatively more important probably depends on the species. There are plants that can achieve high abundance, but only in a few habitat types (e.g. ericaceous shrubs in boreal forest understorey). Other species are widespread and occur in numerous habitats, but not at high abundance (e.g. grass species that occur sparsely in many herbaceous communities).

It is recognized that plants are essentially holobionts – a plant individual with an associated microbiome (Box 1) (Margulis, 1991; Theis *et al.*, 2016). Beneficial and antagonistic microbes may play an important role in determining plant species performance in nature (Bennett & Klironomos, 2019; Kandlikar *et al.*, 2019). It would thus be logical to expect that relationships with microbes differ in a systematic way between winner and loser plant species, and these are the relationships we explore in this review. To reach a clearer understanding, it will be important to consider the roles of microbiomes in altering plant niches and dispersal success, which both contribute to plant geographic occupancy, as well as in changing plant competitive ability, which contributes to local abundance.

Here, we propose a theoretical framework for better understanding how plant species as holobionts become winners. We integrate landscape- and microbiome-level approaches and suggest that landscape structure is a filter that selects for certain microbiome-dependent plant traits. We suggest that the plasticity of symbiotic relationships (Box 1) between plants and their microbiomes could be an important determinant of plant performance at the landscape level.

### Box 1

#### Key terms

*Holobiont*: an individual (here, we consider plant individuals) with an associated microbial community (microbiome).

*Winner*: a species that achieves high global abundance through high local abundance and/or high geographic occupancy.

#### Distribution

*Abundance*: the amount of certain types of organism in a sample (fixed area, volume, mass unit).

*Global abundance*: the total abundance of living individuals of a given species.

*Geographic (global, spatial) occupancy*: the frequency of species occurrence; for example, measured as the number of grid cells on a map where the species (at least one individual) is present.

#### Interactions

*Symbiosis*: a close association (having at least some degree of physical contact) of two or more organisms which is potentially long-lasting, and which benefits at least one partner at least during certain period.

*Symbiont*: an organism which is a partner in symbiotic relationship.

*Symbiont plasticity, symbiotic plasticity*: variation in symbiont function within a holobiont, underpinned by various genetic, ecological and physiological mechanisms.

*Mutualism*: a close association of two or more organisms that benefits all partners. Nutritive (trophic) mutualism contributes to obtaining nutrients from the environment. Defensive mutualism defends host against antagonistic organisms (parasites, pathogens).

*Mutualist*: an organism which is a partner in mutualistic relationship.

*Mutualist flexibility, mutualism flexibility* are synonymous with symbiont plasticity and symbiotic plasticity, except that it describes strictly mutually beneficial biotic interactions.

*Parasitism*: a close antagonistic relationship in which one species is harmed, while the other benefits.

*Parasite*: an organism which receives benefit in parasitic relationship.

*Pathogen*: a parasite which causes significant harm to the host.

*The mutualism–parasitism continuum*: a phenomenon where individuals of the same taxon, or taxa within the same functional group, represent a gradient where the mutual benefit of the interaction gradually turns towards benefit of one partner and harm of another.

#### Landscapes

*Landscape*: an area of land with characteristic structural features, such as topography, vegetation cover, hydrological systems etc.

*Historic landscapes*: those landscapes that have experienced little or no land use change.

*Hybrid landscapes*: those landscapes that have undergone partial ecosystem conversion, resulting in a mosaic of anthropogenic and natural ecosystems.

*Novel landscapes*: those landscapes where natural areas have mostly been converted to intensive agricultural, urban, and industrial land use. This can produce eutrophic conditions due to chemical pollution and climate warming, or oligotrophic conditions due to land overexploitation, leading to degradation.

## II. Environmental context of winning and losing

Plant growth and reproduction are primarily determined by the suitability of plant traits along two gradients, broadly categorized as stress and disturbance (Grime *et al.*, 2007). Stresses include resource availability, as well as conditions, such as temperature or

the presence of toxins that inhibit growth (Grime, 2001). Disturbance describes instability in conditions (Slobotkin & Sanders, 1969). However, it is characteristic of both theoretical and experimental ecology that plant traits are addressed within the context of ecological conditions at certain 'points', such as an experimental unit in the glasshouse. Some studies have considered plant coexistence in heterogeneous experimental systems (Reynolds *et al.*, 2007; Questad & Foster, 2008), but the real environment of plants is heterogeneous not only at the small scale but also at the landscape and regional level. To understand how plant traits really 'work', analysis needs to be placed in a wider spatial context. Landscape-level factors are usually considered in the context of dispersal traits (Haddad *et al.*, 2015; Williams *et al.*, 2016), while the potential of the landscape to act as a selective pressure on competitive ability is not commonly considered. However, this is a critical consideration in understanding species success – if a species exhibits sufficient competitiveness in different patches of a heterogeneous landscape, it might ultimately have greater success than a more specialized competitor that is very successful in certain patches but not in others.

Any landscape (Box 1) can be characterized in terms of the heterogeneity of ecological conditions in time (instability) and space (patchiness), with the latter describing both the occurrence of different types of ecosystem and the occurrence of different dynamic (successional) stages of the same ecosystem. The success of a species in terms of global abundance is determined not only by how it copes with specific conditions at a given location but also by how it copes with landscapes where conditions change in space and time.

There are still landscapes that have experienced little or no anthropogenic land use change. However, the structure of most landscapes has been significantly transformed by human activity (Foley *et al.*, 2005). Some have undergone gradual conversion (e.g. development of seminatural grasslands), where some natural ecosystems remain; others have experienced rapid and extensive conversion (e.g. industrial agriculture). Hobbs *et al.* (2014) introduced the ecosystem novelty framework, which distinguishes historical, hybrid, and novel patches in landscapes and addresses their connectivity and landscape functionality. We upscale novelty from landscape elements to entire landscapes and distinguish three landscape dynamic types (see also Box 1):

(1) Historic landscapes have experienced little or no land use change. In these landscapes, natural ecosystems, such as undisturbed forests or traditionally managed seminatural grasslands, prevail. These landscapes experience natural disturbances, which are typically limited in extent and frequency.

(2) Hybrid landscapes have undergone partial ecosystem conversion. In these landscapes, moderately disturbed natural and seminatural ecosystems co-occur with intensively managed agricultural and urban ecosystems. Between the years 1700 and 2000, the terrestrial biosphere made the transition from mostly wild to mostly anthropogenic, passing the 50% mark early in the 20<sup>th</sup> century, and since then remaining wilderness areas have rapidly declined in extent and become fragmented (Ellis *et al.*, 2013; Watson James *et al.*, 2016; Allan *et al.*, 2017; Jacobson *et al.*, 2019). Hybrid landscapes, combining anthropogenic and

natural ecosystems, have become dominant on Earth (Ellis *et al.*, 2013; Watson James *et al.*, 2016).

(3) Novel landscapes have experienced the most rapid and extensive conversion. In these landscapes, disturbed natural and seminatural ecosystems may occur as small fragments, but are mostly converted into intensive agricultural, urban and industrial land use (Foley *et al.*, 2005). The species composition of novel ecosystems is typically completely transformed in comparison with the historic system (Hobbs *et al.*, 2014). Co-occurring species might not be native to the geographic location and might exhibit different functional properties than aboriginal species (Schittko *et al.*, 2020).

As a result of changes in land use regime (Thuiller *et al.*, 2008; Sirami *et al.*, 2017; Dullinger *et al.*, 2021), novel landscapes may change in contrasting directions, reaching different steady states. On one hand, eutrophic novel landscapes develop under disturbances that release resources and enhance 'greening' (Zhu *et al.*, 2016; Huang *et al.*, 2018). On the other hand, there are many landscapes where ecosystems suffer from heavy grazing, fire, erosion, forest clearcutting and subsequent runoff, irrigation and subsequent salinization. (D'Odorico *et al.*, 2013; Wan *et al.*, 2021). Such disturbances produce oligotrophic novel landscapes.

Critically, landscape types also differ in terms of their patchiness. Historical landscapes are relatively uniform, with prevailing environmental conditions changing only due to natural gradients, including the natural disturbance regime (Jentsch & White, 2019). By contrast, hybrid landscapes are characterized by strong patchiness associated with different stages in land use transition (Foley *et al.*, 2005). In these landscapes, natural and seminatural landscape elements co-occur with anthropogenic elements (Fischer & Lindenmayer, 2007). Novel landscapes are products of severe human impact and exhibit low to intermediate spatial patchiness simply because most natural and seminatural ecosystems have been replaced by relatively homogeneous novel anthropogenic ecosystems (Karp *et al.*, 2012; Aronson *et al.*, 2016).

### III. Plant functional types in landscapes

Different life history strategies are expected to be successful in different environmental settings. Classical community theory suggests that specialist species can be locally abundant in the conditions that favour them, while generalists are favoured in variable environmental conditions but usually do not exhibit high local abundance (MacArthur, 1972). This pattern is assumed to be driven by the costs associated with being a specialist or a generalist (organisms can adapt to specific conditions and achieve high fitness in these conditions but at the cost of losing fitness elsewhere), and it should result in a negative relationship between local abundance and geographic occupancy. This principle, sometimes called 'a jack of all trades is a master of none', was challenged by Brown (1984), who reported a positive relationship between local density and range size and suggested that the 'jack of all trades can be master of all'. However, subsequent analyses found no convincing empirical evidence of this (Gaston *et al.*, 1997). Hence, globally successful species might be particularly associated with one part of the space described by the trade-off (e.g. with locally abundant but narrowly

distributed species; or with locally rare but widespread species) or with those species that manage to circumvent the trade-off to some degree (i.e. achieve relatively high local abundance despite having relatively wide occurrence).

In plant ecology, the ‘jack of all trades’ hypothesis has not been explicitly addressed. Vela Díaz *et al.* (2020) found no correlation between local abundance and geographic occupancy among plants. Other studies investigating the characteristics of specialist and generalist species found that specialist species tend to be stress tolerant and abundant in extreme environments, while generalists dominate in more benign, intermediate conditions along environmental gradients (Boulangéat *et al.*, 2012; Carboni *et al.*, 2016; Zeleny & Chytrý, 2019). Staudé *et al.* (2022) surveyed the dynamics of 1827 European plant species during several decades and found increases in the occupancy of generalist species, and more nutrient-demanding species, which are also strong competitors in eutrophic conditions. Invasive species also tend to be more eutrophic, compared to their noninvasive congeners (Davidson *et al.*, 2011).

In homogeneous landscapes, the same traits that underlie local abundance in one location are also successful elsewhere because environmental conditions are similar. Thus, if there is a species that copes well with local conditions, it has the potential to become widely abundant in homogeneous conditions at a larger spatial scale. In heterogeneous landscapes, however, it seems that the ‘jack of all trades’ should either be ‘master of none’ as suggested by MacArthur (1972) or ‘master of some (e.g. eutrophic) conditions’ as suggested by Davidson *et al.* (2011) and Staudé *et al.* (2022).

It is as yet poorly understood which traits enable plant species to occupy a wide niche, that is be a generalist. Phenotypic plasticity, that is the ability of a genotype to adjust its phenotype in response to environmental variation (Bradshaw, 1965), must be key to achieving a wide ecological niche and, hence, high geographic occupancy (Davidson *et al.*, 2011; Eriksson & Rafajlović, 2022; Goldberg & Price, 2022). However, quantification of adaptive phenotypic plasticity that should widen the niche is challenging empirically due to the many traits that can exhibit plasticity and a portion of phenotypic variation being maladaptive (van Kleunen & Fischer, 2005; Hulme, 2008). So far, no clear empirical evidence has been found to connect phenotypic plasticity to either local abundance or geographic occupancy (Pohlman *et al.*, 2005; Dostal *et al.*, 2016). Similarly, studies often fail to detect a cost to plasticity, which would explain the existence of habitat specialists (Schneider, 2022). It is possible that we have not yet identified the traits whose plasticity is most important for plant distribution and success. It is in this context that we consider the role of the microbiome.

#### IV. Holobionts

The appreciation that microbiomes significantly influence the distribution and abundance of macroorganisms represents a substantial paradigm shift in ecology. Among plant-associated microbiota, bacteria and fungi are the most dominant forms, but other groups – including archaea, algae, nematodes, and protists – also impact plant functioning and health (Trivedi *et al.*, 2020). The

so-called holobiont is a complex symbiotic entity of close and prolonged associations between plant and microbial organisms inhabiting the leaf, stem, and root endosphere, phyllosphere and rhizosphere (Hacquard & Schadt, 2015). Associated microorganisms often span the mutualist parasite (Box 1) continuum (Johnson & Graham, 2013; Smith & Smith, 2015; Hawkes *et al.*, 2020; Mengistu, 2020; Benning & Moeller, 2021), and their net effect depends on ecological conditions. The mutualistic part of the microbiome potentially ensures key functions for holobiont fitness, by promoting the nutrition and health of the plant (Lemanceau *et al.*, 2017) and improving its ability to withstand the negative effect of parasites, including pathogens (Veresoglou & Rillig, 2012; Pérez-de-Luque *et al.*, 2017; Bass *et al.*, 2019). Plant microbiomes thus significantly influence the growth of host plants at the individual and population level (Tedersoo *et al.*, 2020; Zhan *et al.*, 2022), with consequences for plant community composition and structure (Bennett & Klironomos, 2019; Kandlikar *et al.*, 2019; Tedersoo *et al.*, 2020). In this review, we focus particularly on soil organisms. However, this is simply a reflection of where existing evidence is available, and we see no reason why many of the principles and processes we discuss should not apply also to the aboveground part of the holobiont.

The local performance of plant species depends on plant life history characteristics (Grime, 2001; Westoby *et al.*, 2002; Grime *et al.*, 2007). Geographic occupancy, in turn, is expected to be enhanced by high phenotypic plasticity, which should facilitate range expansion over patchy environments (Eriksson & Rafajlović, 2022), though empirical support for this prediction is weak. Interestingly, Gibert *et al.* (2019) showed that plant traits were poor predictors of the characteristics of plant symbiotic associations. Thus, if symbiosis impacts a plant’s performance, its effect might not go hand in hand with conventional plant life history traits. Rather, symbiotic interactions might play an important but underappreciated role in enhancing (or harming) plant performance across large spatial scales and thus potentially defining distribution areas.

#### V. Symbiont plasticity

Holobionts are not stable deterministic systems where a fixed set of organisms always associates with each other; rather the number, composition, and functioning of microbes can vary in time and space. Wernegreen & Wheeler (2009) introduced the concept of ‘symbiont plasticity’ to encompass the genetic, ecological and physiological mechanisms that generate variation in symbiont functions within a holobiont. Later authors addressed the same topic in the context of flexible mutualism (Moora, 2014; van der Heide *et al.*, 2021). For example, it has been found that the rate of plant root colonization by AM fungi exhibits higher variation in facultatively mycorrhizal species (Soudzilovskaia *et al.*, 2020). Liang *et al.* (2023) showed that plants with thick roots are consistently well colonized by mutualistic fungi, while those with medium or thin roots display a wide range of colonization intensity.

Plants have evolved complex metabolite-mediated strategies, including those acting via the immune system, to selectively recruit beneficial microorganisms in their microbiota and suppress

harmful microbes; either directly or via facilitation of microbes that restrict the proliferation of strong parasites (Hacquard *et al.*, 2017; Mesny *et al.*, 2023). Plants possessing these strategies are able to influence the relative proportions of different microbiome members or lead some microbes to disappear and others to colonize. In principle, such symbiont plasticity may potentially improve plant fitness in the following ways:

### 1. Cost regulation

Symbiont plasticity allows plants to optimize their energetic costs when mutualisms change in the benefit they confer or even become parasitic. For instance, plants suppress and even prevent AM root colonization in fertile soil (Koide & Schreiner, 1992; Pozo *et al.*, 2015; Cosme *et al.*, 2018; Nouri *et al.*, 2021). Similarly, rhizobial nitrogen-fixing plants downregulate mutualism when there is sufficient nitrogen in the soil (Menge *et al.*, 2015; Dovrat & Sheffer, 2019). Plants are also able to prevent colonization by certain leaf endophytes, although the conditions in which this occurs remain somewhat unclear (González-Teuber *et al.*, 2020).

Conversely, plants may boost mutualistic activity in conditions where the use of nutritive mutualism is beneficial and cost-efficient. For instance, tropical leguminous trees intensify mutualistic N fixation and increase in abundance in early successional stages where there is abundant light (Taylor *et al.*, 2019); in mature successional stages light becomes limited and nitrogen fixation becomes too costly, but by that stage, the trees can persist in the absence of the mutualism (Houlton *et al.*, 2008; Menge *et al.*, 2014; Menge & Chazdon, 2016). Plants may also upregulate their defence signalling by boosting the abundance of bacteria in their rhizosphere in response to pathogen attack, as was recently demonstrated in a system comprising wheat plants, the growth-promoting bacterium *Stenotrophomonas rhizophila* and the fungal pathogen *Fusarium pseudograminearum* (Liu *et al.*, 2021).

### 2. Switch of function

Symbiont plasticity may allow a switch of mutualism from one function to another, for example from a nutritive to a defensive function. Such switching was hypothesized by Lekberg *et al.* (2021), who found that N fertilization increased the amount of pathogens in the ecosystem, but simultaneously the share of root colonizing edaphophilic (allocating hyphae primarily into the soil) AM fungi decreased and that of rhizophilic fungi (allocating hyphae primarily into roots) increased. Such a pattern is likely to reflect switching between partners that offer either resource acquisition or pathogen protection (Weber *et al.*, 2019; Marro *et al.*, 2022); but it might potentially also reflect a switch in the symbiotic function offered by individual microbial partners. However, knowledge about symbiotic function switching is scarce. Some soil-borne fungi, such as taxa from the genus *Armillaria* (Basidiomycota) (reviewed by Baumgartner *et al.*, 2011), have a lifestyle with both saprotrophic and pathogenic stages, but to the best of our knowledge, it is unknown whether host plants can regulate the switch, for example switching a pathogen back to being a saprotroph.

### 3. Partner receptivity

The ability to cope with alternative partners in situations where there are no preferred partners is another facet of symbiont plasticity. This phenomenon may enhance establishment after dispersal into a new area and hence increase occupancy. For instance, mutualist partner limitation has been observed for ectomycorrhizal (Haskins & Gehring, 2005; Shemesh *et al.*, 2020; Nuske *et al.*, 2021), arbuscular mycorrhizal (Weber *et al.*, 2005; Carteron *et al.*, 2020) and nitrogen-fixing (Eisenlord *et al.*, 2012; Simonsen *et al.*, 2017; Grman *et al.*, 2020) plants. Conversely, wide partner receptivity of plant species towards ectomycorrhizal fungi (Pither *et al.*, 2018; Vlk *et al.*, 2020) or rhizobial bacteria (Klock *et al.*, 2015), or generally of symbiotic fungi and bacteria (Ramirez *et al.*, 2019) contributes to range expansion.

## VI. Holobionts as winners

McKinney & Lockwood (1999) associated losers with specialists and winners with generalists. More generally, for winners as species that maximize global abundance (*sensu* Preston, 1948), there are two ways to achieve it: either species that are competitive in certain conditions but not common must broaden their niche and improve their dispersal ability and efficiency (ability to establish upon arrival), or widely distributed but locally nonabundant species must become better competitors, at least in certain conditions.

We hypothesize that symbiont plasticity is an overlooked mechanism that can contribute to a wider abiotic and biotic niche, more efficient establishment upon dispersal, and higher competitive ability of plant holobionts in contemporary landscapes, ultimately leading some plant species to become winners. Symbiotic plasticity of plant holobionts may be expressed via adapting the type and level of mutualism according to (1) the level of environmental resources (cost regulation), (2) the presence of parasitic organisms (switch of function), or (3) the presence of mutualistic partners (partner receptivity). Thus, plasticity allows plants to regulate mutualism according to the characteristics of the local abiotic and biotic environment. We suggest three mechanisms through which symbiont plasticity contributes to wider geographic occupancy and one mechanism contributing to higher local abundance (Fig. 1).

#### 1. Abiotic niche expansion

Symbiont plasticity with respect to the resource level of the environment allows upregulation of nutritive mutualism when resources are in deficiency and downregulation when resources are in surplus. This allows plants to occupy a wider section of the soil fertility gradient. In the less fertile part, mutualism can overcome the deficiency of resources while in the fertile part suppression of symbiosis reduces costs to the plant.

#### 2. Biotic niche expansion

Plasticity of the plant holobiont also comprises wide receptivity of mutualistic partners, which makes occupancy of new habitats by a

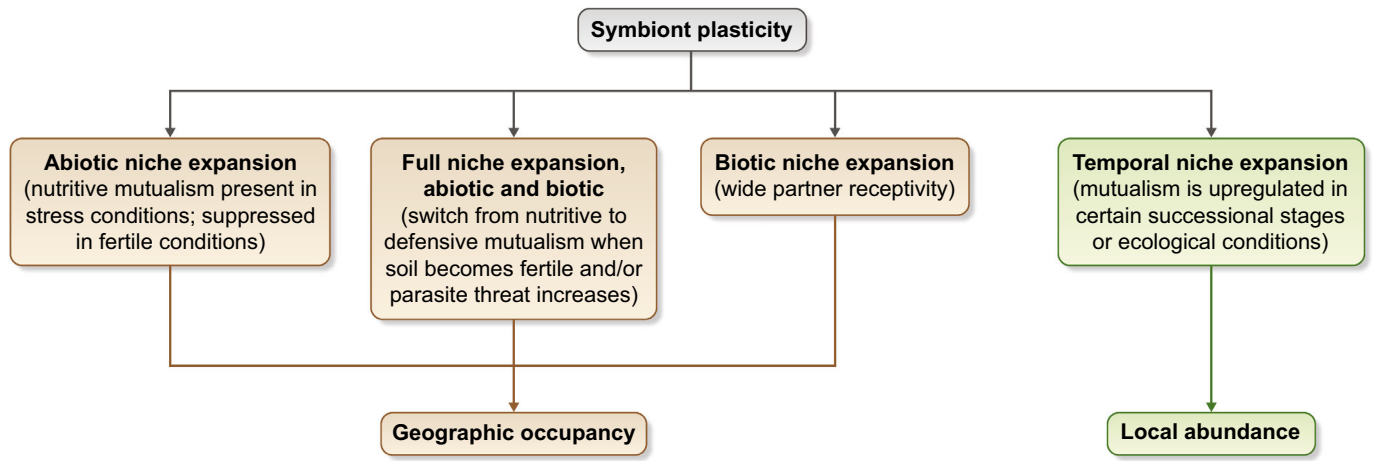


Fig. 1 Conceptual framework linking symbiont plasticity with local abundance and geographic occupancy.

plant less dependent on the presence of preferred mutualist partners. This phenomenon may significantly contribute to successful plant establishment upon dispersal and hence enhance occupancy.

### 3. Full niche expansion due to switching mutualism

Full niche expansion due to switching mutualism is another mechanism enabling plant holobionts to exploit wider sections of the soil fertility and perhaps also climatic gradients. It describes a plant's ability to simultaneously reduce one type of mutualism while increasing another, depending on the local abiotic and biotic pressures. In plants, this primarily means downregulation of nutritive mutualism and upregulation of defensive mutualism in productive environments that typically also harbour more pathogens. Hence the abiotic niche broadens along the soil fertility gradient and the biotic niche expands in relation to parasite community characteristics (abundance, composition, diversity).

### 4. Temporal niche expansion

Flexible mutualism allows plants to achieve high local abundance in temporally dynamic ecological conditions, where mutualism is highly beneficial only in some stages. Tropical leguminous trees serve as examples: they persist in all successional stages but use mutualism to gain high abundance only in early successional stages where light is not limiting. N fixation declines from mid-successional stages onward as light becomes limited.

## VII. Holobionts in landscapes

In order to succeed both locally and globally, plant species must cope with conditions in their immediate surroundings and in the landscape as a whole. The conventional approach considers interaction-related plant traits in the context of local performance, while dispersal traits and biogeographic processes are addressed when explaining geographic occupancy. We propose that symbiont

plasticity can contribute to the overall success of plant species in conditions of ongoing global change. Reflecting the lack of empirical studies specifically addressing these topics, we aim to synthesize existing indirect evidence and make hypothetical predictions to serve as a basis for future research.

### 1. Historic landscapes

Historic landscapes represent 'true nature' where landscape features are dependent on natural climatic and soil factors, disturbance regime, and biogeographic history. In these landscapes, different kinds and numbers of mutualistic and parasitic microbes occur in different environmental settings (Arnold & Lutzoni, 2007; Thrall *et al.*, 2007; Semmartin *et al.*, 2015; Větrovský *et al.*, 2019; Harrison & Griffin, 2020; Makiola *et al.*, 2022; Marro *et al.*, 2022).

In historic landscapes, local plant dominants may become common over a large spatial scale if the landscape is homogeneous in space, that is similar ecological conditions can be found over large areas (Zobel *et al.*, 2023). Achieving wide distribution in naturally homogeneous landscapes, such as extensive areas of boreal forest, tropical rain forest, dry temperate grassland, or savannah, does not directly require plasticity in the sense that conditions do not vary significantly. In these areas, a nonplastic plant species that is locally abundant in the vegetation type may also become geographically widespread. However, if the area is naturally heterogeneous, for example due to patchy parent rock or diverse topography, symbiont plasticity potentially favours wide geographic occupancy for the reasons described above.

### 2. Hybrid landscapes

Hybrid landscapes have become dominant on Earth, so it is necessary to identify their specific characteristics when determining potentially winning species in current conditions. Compared with historic landscapes, hybrid landscapes are spatially more heterogeneous, both in terms of abiotic (Vitousek, 1994; Foley *et al.*, 2005; Fischer & Lindenmayer, 2007) and biotic

(Honnay *et al.*, 2005; Kieseewetter & Afkhami, 2021; Kieseewetter *et al.*, 2023) conditions, as natural and anthropogenic ecosystems intermingle. In hybrid landscapes, highly specialized species may exhibit high abundance in suitable patches, while generalists may be present in many patches but at low abundance. To improve performance locally and regionally in heterogeneous hybrid landscapes, plants must enhance their competitive ability, at least in certain environmental conditions, or expand their niche and improve dispersal efficiency. As plants may experience mutualist limitation during range expansion or invasion (Bogar *et al.*, 2015; Simonsen *et al.*, 2017; Batstone *et al.*, 2018; Benning & Moeller, 2021; Nuske *et al.*, 2021), broadening of the biotic niche may enhance establishment after dispersal to a new area and thus contribute to the occupancy of plant species in hybrid landscapes.

These outcomes can be accomplished via symbiont plasticity, meaning that ‘mutualistic nutritive and defensive support’ is provided by the microbiome in situations where it is most critical for the plant host and avoided in situations where it is too cost-inefficient. Indeed, there is evidence that plasticity in mutualistic interactions can contribute to broadening the abiotic niche, both towards oligotrophic conditions (Afkhami *et al.*, 2014) and towards eutrophic (Gerz *et al.*, 2018), or simultaneously broadening both abiotic and biotic niche via switching mutualism (Lekberg *et al.*, 2021). In addition, recent studies have shown that alien plants with flexible mutualistic interactions have become more widespread than inflexible ones (Menzel *et al.*, 2017; Moyano *et al.*, 2020). Similarly, plants can expand their niche via altered interactions with growth-promoting bacteria, but there is very limited information available about the processes due to the lack of accurate and cost-effective methods for evaluating the activity of these bacteria in the natural environment (reviewed by Rilling *et al.*, 2019).

### 3. Novel eutrophic landscapes

Considering the net costs and benefits of a plant living together with a symbiont often indicates that there is a mutualism–parasitism continuum (Smith & Smith, 2015). For instance, the microbial partners that can be classified as nutritive mutualists in infertile conditions may act as parasites in fertile soil conditions (Johnson & Graham, 2013; Mandyam & Jumpponen, 2015; Smith & Smith, 2015), such as those encountered in novel eutrophic landscapes. Consequently, it might be useful for potential winners to exhibit symbiotic plasticity and limit the extent (Amijee *et al.*, 1989; Corkidi *et al.*, 2002; Zheng *et al.*, 2018) or activity (Dovrat & Sheffer, 2019) of the association or to perform without a symbiotic partner altogether (Lü *et al.*, 2020). Nonmycorrhizal plant species (Formenti *et al.*, 2023), which are an example of the latter, typically occur in disturbed habitats, where competition with other plants is low and soil nutrient availability is high (Lambers & Teste, 2013). Since novel landscapes are expected to be significantly less patchy than hybrid landscapes due to the almost complete absence of natural and seminatural habitats, characteristics underlying local dominance may also largely ensure a high geographic occupancy of species.

In novel eutrophic landscapes, the occurrence and abundance of plant pathogens increases relative to those of mutualistic microbes (Helgason *et al.*, 1998; Fox *et al.*, 2007; Veresoglou *et al.*, 2013; Lekberg *et al.*, 2021; Singh *et al.*, 2023). In such conditions, switching mutualism might be a vital strategy. For instance, plants reduce carbon allocation to AM fungal taxa with extensive external hyphae while fungi allocating biomass inside roots remain (Treseder *et al.*, 2018) or even increase (Lekberg *et al.*, 2021). The remaining fungi fulfil primarily defensive functions, for instance by occupying the free space (Sikes *et al.*, 2009). In addition, fungi may induce phenolic-based plant defences (Frew & Wilson, 2021), although the relative costs of such plant defences with and without fungal participation remain to be established.

### 4. Novel oligotrophic landscapes

Novel oligotrophic landscapes are characterized by low nutrient availability in soil and spatial homogeneity – virtually no former natural and seminatural habitats remain. Hence, nutritive mutualism such as AM (Marro *et al.*, 2022) and rhizobial nitrogen fixation (Oldroyd & Leyser, 2020), may enhance plant performance. However, degradation due to overgrazing (Cavagnaro *et al.*, 2019; Yang *et al.*, 2020) and aridification (Berdugo *et al.*, 2020) can result in a reduction of mutualistic and an increase of parasitic microbes. In conditions where mutualist microbes are in shortage, high receptivity provides an advantage for both native (Batstone *et al.*, 2018) and invasive (Klock *et al.*, 2015) plant species. In certain highly impoverished ecosystems, host species do not use nutritive mutualism but instead possess a range of root innovations that allow them to mine soil nutrients, such as proteoid or cluster roots, and dauciform roots (Lambers & Teste, 2013). However, these innovations confer less protection against pathogens. Thus, there is a trade-off between efficient nutrient uptake via specialized ‘mutualist free’ root structures and pathogen protection, which may explain why vegetation on highly nutrient-impoorished soils can be co-dominated by nonmycorrhizal and mycorrhizal species (Albornoz *et al.*, 2017; Raven *et al.*, 2018). The latter might benefit from symbiont plasticity with respect to broad partner receptivity and switching between mutualists with different functions, but we are unaware of empirical evidence.

## VIII. Empirical illustration

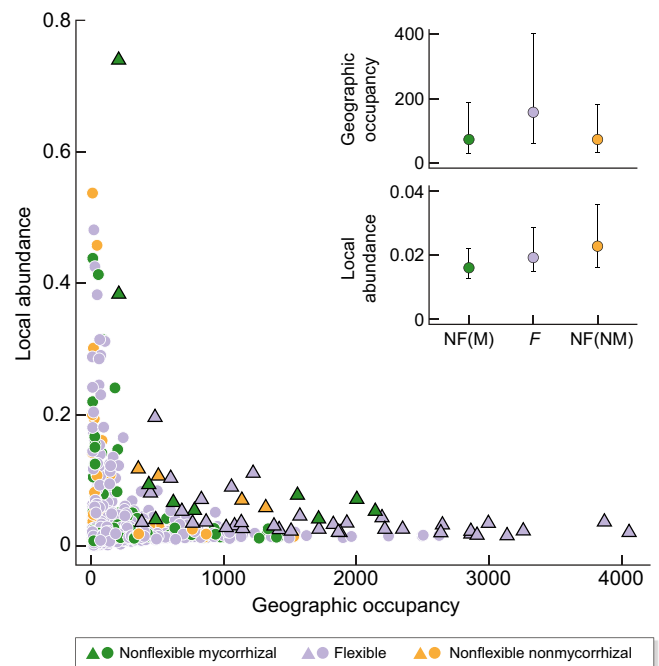
We suggested that high local abundance is related to specialized adaptations to local conditions. These adaptations may include nonflexible nutritive mutualism in nutrient-limited systems and absence of nutritive mutualism in conditions where its use is not cost-efficient. At the same time, high geographic occupancy is expected to relate to high symbiont plasticity. Consequently, one may expect that high local abundance can be achieved by plant species whose symbiotic relationships with various types of microbes fit the best for these particular conditions, but plant species possessing symbiotic plasticity should be overrepresented among species with wide geographic occupancy.

To illustrate these ideas, we investigated the presence of one of the most common mutualisms – AM – among successful plants.

Because AM-related plasticity in plants has not been screened experimentally in a systematic manner, we must use descriptive data, which are expected, to some extent, to characterize flexibility with respect to formation of AM, and thus a form of symbiont plasticity. Here, we used the relative number of studies reporting a given species as either colonized by AM fungi or exhibiting nonmycorrhizal status, as presented by Bueno *et al.* (2017). We distinguished between nonflexible mycorrhizal species (all available records reported mycorrhizal status), nonflexible nonmycorrhizal species (mycorrhizal status not reported), and flexible species (some studies report mycorrhizal and other studies nonmycorrhizal status).

We estimated different metrics of plant species abundance from sPlotOpen – a global vegetation plot database (Sabatini *et al.*, 2021), which is an open-access, geographically and ecologically balanced, version of the much larger sPlot database. It contains 95 104 plots and 1945 385 species occurrences. In order to assess a methodologically homogeneous sample, we considered only largely herbaceous plots (45 735) by excluding plots described as ‘forest’ (the methods of estimating the abundance of trees were very different across the samples). The plot level data comprise estimates of relative cover or abundance (hereafter abundance) for each species recorded in the plot. We calculated local abundance (median plot level abundance; for species present in  $\geq 10$  plots), geographic occupancy (the number of plots occupied), and global abundance (cumulative abundance in the data set) for all species in the data set.

In the sPlotOpen database, vegetation plots from Europe and North America dominate (Sabatini *et al.*, 2021). Because there are few historic landscapes left, especially in Europe, but also in many other parts of the world covered by the data set, we have reason to expect that most of the plots come from the hybrid landscape category. We found that locally abundant species represented a fairly even mixture of always (36%), flexibly (36%) and not (28%) mycorrhizal species; widespread species were predominantly flexible (84%); and globally abundant species also tended to be flexible (but not to such a great extent, 76%) (Supporting Information Fig. S1). The identities of widespread and globally abundant species overlapped to a large extent (29/50 species in each were shared), while relatively few locally abundant species were also globally abundant (3/50), and no species appeared in all three categories (locally abundant, geographically widespread, globally abundant). When considering all species for which mycorrhizal information was available, we found that putatively flexible species were characterized by the highest geographic occupancy (Fig. 2). While no species were able to achieve both relatively high local abundance and geographic occupancy, the species with the highest global abundance were positioned on the upper margin of the data cloud (the 50 species with the highest global abundance are marked with triangles in Fig. 2), indicating that both local abundance and especially geographic occupancy were to a certain extent maximized. Overall, the results agreed with our prediction that flexible mutualism is associated with wider global distribution, but also with higher global abundance.



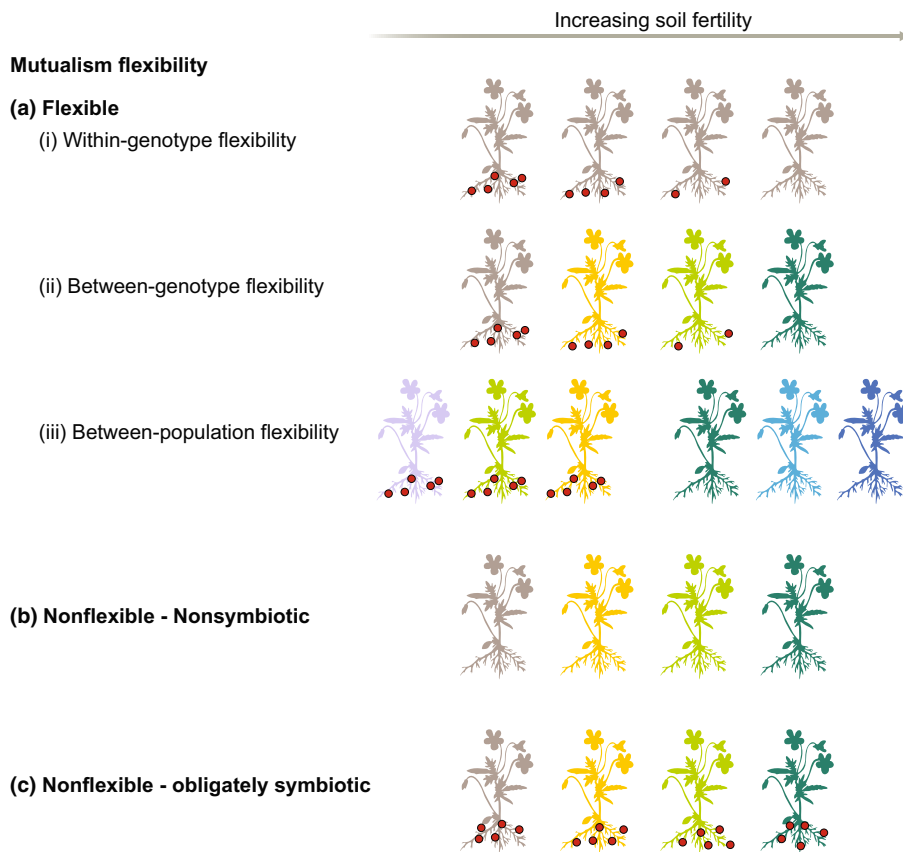
**Fig. 2** Abundance, occupancy and mycorrhizal flexibility of species in herbaceous vegetation plots in the sPlotOpen database. Local abundance was calculated as median plot level abundance (in species present in  $\geq 10$  plots), geographic occupancy—the number of plots occupied, and global abundance—cumulative abundance in the data set. Mycorrhizal flexibility (*F*, flexible; *NF(M)*, nonflexible mycorrhizal; *NF(NM)*, nonflexible nonmycorrhizal) could be assigned to 2144 species (*F* = 661 (31%); *NF(M)* = 1142 (53%); *NF(NM)* = 334 (16%)). The relationship between species local abundance and geographical occupancy is displayed with different mycorrhizal flexibility types distinguished. Inset panels show the median (point) and interquartile range (bars) of local abundance and occupancy for species of different mycorrhizal flexibility. Triangular symbols identify the 50 species with the highest global abundance.

## IX. Synthesis and perspectives

The global success or failure of plant species can be explained by combining approaches from traditional plant ecology with those from landscape and microbial ecology.

In recent centuries, human activity has been the most influential force shaping the environment, giving rise to patchy hybrid landscapes, where different natural and anthropogenic, often eutrophic, ecosystems co-occur, or novel landscapes, where anthropogenic ecosystems prevail. In these conditions, species with broad niches and sufficient competitive ability in eutrophic conditions are expected to show the highest global abundance.

Phenotypic plasticity may be key to achieving a broad realized niche. However, when addressing plant plasticity and distribution, holobiont characteristics are rarely considered. Symbiont plasticity – the capacity to adopt symbiotic interactions according to the demands of the environment – may allow plants to expand their abiotic and biotic niches, and to boost competitive ability in certain conditions (Fig. 1). Currently, there is very little empirical data on symbiont plasticity. Further studies should provide more empirical



**Fig. 3** Manifestation of symbiont plasticity, expressed as root mutualist flexibility. Variation in the rate of root colonization (represented by red points) among (a) flexible (b) nonflexible (nonsymbiotic) and (c) nonflexible (obligate symbiont) plant species. Among flexible species, flexibility may be manifested (i) within genotypes, (ii) between genotypes and (iii) between populations. Different colours represent different genotypes within a given mutualism flexibility type.

information and, in particular, provide answers to the following focused questions:

(1) Does the relationship between local abundance and geographic occupancy of species differ between different types of holobionts such as plant species of different mycorrhizal type and status, nitrogen fixers, plants associated with systemic vertically transmitted endophytes etc.?

(2) At what scale does symbiont plasticity manifest itself? Is regulation of the amount and activity of symbionts expressed primarily as phenotypic plasticity *sensu stricto* (i.e. the ability of individual genotypes to express different phenotypes) or does it also vary among genotypes within a population (some genotypes always exhibit mutualistic phenotypes and others are nonsymbiotic) or across populations due local adaptation (some populations are colonized by symbionts and others are not, Fig. 3). In this case, mutualism flexibility may be an appropriate term to incorporate phenotypic plasticity and other genetic mechanisms underlying variation in plant mutualist interactions.

(3) How different is the degree of symbiont plasticity among plant species, does it correlate with other, well-known plant functional traits, and how strong is the underlying phylogenetic signal? Unambiguous criteria and a standardized test for evaluating symbiont plasticity must be developed to compare different species.

(4) How is the taxon composition of symbiotic microbes related to function? To what degree is symbiont plasticity related to a host plant's active regulation of the composition of the microbiome? Can plants regulate microbiome composition to the degree that

there is a change in function, for example a switch among mutualists from nutritive to defensive function? Can individual microbial taxa provide different functions depending on the environmental context or in response to plant regulation?

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## Competing interests

None declared.




## Author contributions

MZ designed the outline of the review and wrote the first draft. JD performed the data analyses and drew the figures. MZ, KK, MM, MS and JD reviewed and edited the manuscript.

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## References

- Afkhami ME, Rudgers JA, Stachowicz JJ. 2014. Multiple mutualist effects: conflict and synergy in multispecies mutualisms. *Ecology* 95: 833–844.
- Albornoz FE, Burgess TI, Lambers H, Etchells H, Laliberté E. 2017. Native soilborne pathogens equalize differences in competitive ability between plants of contrasting nutrient-acquisition strategies. *Journal of Ecology* 105: 549–557.
- Allan JR, Venter O, Watson JEM. 2017. Temporally inter-comparable maps of terrestrial wilderness and the Last of the Wild. *Scientific Data* 4: 170187.
- Amijee F, Tinker PB, Stribley DP. 1989. The development of endomycorrhizal root systems. VII. A detailed study of effects of soil phosphorus on colonization. *New Phytologist* 111: 435–446.
- Arnold AE, Lutzoni F. 2007. Diversity and host range of foliar fungal endophytes: Are tropical leaves biodiversity hotspots? *Ecology* 88: 541–549.
- Aronson MFJ, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M *et al.* 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97: 2952–2963.
- Bass D, Stentiford GD, Wang H-C, Koskella B, Tyler CR. 2019. The pathobiome in animal and plant diseases. *Trends in Ecology & Evolution* 34: 996–1008.
- Batstone RT, Carscadden KA, Afkhami ME, Frederickson ME. 2018. Using niche breadth theory to explain generalization in mutualisms. *Ecology* 99: 1039–1050.
- Baumgartner K, Mpa C, Hoffmeister D. 2011. Secrets of the subterranean pathosystem of Armillaria. *Molecular Plant Pathology* 12: 515–534.
- Bennett JA, Klironomos J. 2019. Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. *New Phytologist* 222: 91–96.
- Benning JW, Moeller DA. 2021. Microbes, mutualism, and range margins: testing the fitness consequences of soil microbial communities across and beyond a native plant's range. *New Phytologist* 229: 2886–2900.
- Berdugo M, Delgado-Baquerizo M, Soliveres S, Hernández-Clemente R, Zhao Y, Gaitán JJ, Gross N, Saiz H, Maire V, Lehman A *et al.* 2020. Global ecosystem thresholds driven by aridity. *Science* 367: 787–790.
- Bogart LM, Dickie IA, Kennedy PG. 2015. Testing the co-invasion hypothesis: ectomycorrhizal fungal communities on *Alnus glutinosa* and *Salix fragilis* in New Zealand. *Diversity and Distributions* 21: 268–278.
- Boulangéat I, Lavergne S, Van Es J, Garraud L, Thuiller W. 2012. Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography* 39: 204–214.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. In: Caspari EW, Thoday JM, eds. *Advances in genetics*. New York, NY, USA: Academic Press, 115–155.
- Brown JH. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255–279.
- Bueno CG, Moora M, Gerz M, Davison J, Öpik M, Pärtel M, Helm A, Ronk A, Kühn I, Zobel M. 2017. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography* 26: 690–699.
- Carboni M, Zelený D, Acosta ATR. 2016. Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. *Journal of Vegetation Science* 27: 892–903.
- Carteron A, Parasquive V, Blanchard F, Guilbeault-Mayers X, Turner BL, Vellend M, Laliberté E. 2020. Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests. *Journal of Ecology* 108: 931–944.
- Cavagnaro RA, Pero E, Dudinszky N, Golluscio RA, Grimoldi AA. 2019. Under pressure from above: overgrazing decreases mycorrhizal colonization of both preferred and unpreferred grasses in the Patagonian steppe. *Fungal Ecology* 40: 92–97.
- Corkidi L, Rowland D, Johnson NC, Allen EB. 2002. Nitrogen fertilization alters the functioning of arbuscular mycorrhizas at two semiarid grassland. *Plant and Soil* 240: 310–399.
- Cosme M, Fernández I, Van der Heijden MGA, Pieterse CMJ. 2018. Non-mycorrhizal plants: the exceptions that prove the rule. *Trends in Plant Science* 23: 577–587.
- Darwin C. 1859. *On the origin of species by means of natural selection*. London, UK: John Murray.
- Davidson AM, Jennions M, Nicotra AB. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419–431.
- D'Odorico P, Bhattachan A, Davis KF, Ravi S, Runyan CW. 2013. Global desertification: drivers and feedbacks. *Advances in Water Resources* 51: 326–344.
- Dostal P, Fischer M, Prati D. 2016. Phenotypic plasticity is a negative, though weak, predictor of the commonness of 105 grassland species. *Global Ecology and Biogeography* 25: 464–474.
- Dovrat G, Sheffer E. 2019. Symbiotic dinitrogen fixation is seasonal and strongly regulated in water-limited environments. *New Phytologist* 221: 1866–1877.
- Dullinger I, Essl F, Moser D, Erb K, Haberl H, Dullinger S. 2021. Biodiversity models need to represent land-use intensity more comprehensively. *Global Ecology and Biogeography* 30: 924–932.
- Eisenlord SD, Zak DR, Upchurch RA. 2012. Dispersal limitation and the assembly of soil Actinobacteria communities in a long-term chronosequence. *Ecology and Evolution* 2: 538–549.
- Ellis EC, Kaplan JO, Fuller DQ, Vavrus S, Klein Goldewijk K, Verburg PH. 2013. Used planet: A global history. *Proceedings of the National Academy of Sciences, USA* 110: 7978–7985.
- Eriksson M, Rafajlović M. 2022. The role of phenotypic plasticity in the establishment of range margins. *Philosophical Transactions of the Royal Society, B: Biological Sciences* 377: 20210012.
- Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265–280.
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Stuart Chapin F, Coe MT, Daily GC, Gibbs HK *et al.* 2005. Global consequences of land use. *Science* 309: 570–574.
- Formenti L, Iwanycki Ahlstrand N, Hassemer G, Glauser G, van den Hoogen J, Ronsted N, van der Heijden M, Crowther TW, Rasmann S. 2023. Macroevolutionary decline in mycorrhizal colonization and chemical defense responsiveness to mycorrhization. *iScience* 26: 106632.
- Fox JE, Gullledge J, Engelhaupt E, Burow ME, McLachlan JA. 2007. Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. *Proceedings of the National Academy of Sciences, USA* 104: 10282–10287.
- Frew A, Wilson BAL. 2021. Different mycorrhizal fungal communities differentially affect plant phenolic-based resistance to insect herbivory. *Rhizosphere* 19: 100365.
- Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J. 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* 92: 1156–1173.
- Gaston KJ, Blackburn TM, Lawton JH. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology* 66: 579–601.
- Gerz M, Bueno CG, Ozinga WA, Zobel M, Moora M. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology* 106: 254–264.
- Gibert A, Tozer W, Westoby M. 2019. Plant performance response to eight different types of symbiosis. *New Phytologist* 222: 526–542.
- Goldberg EE, Price TD. 2022. Effects of plasticity on elevational range size and species richness. *The American Naturalist* 200: 316–329.
- González-Teuber M, Vilo C, Guevara-Araya MJ, Salgado-Luarte C, Gianoli E. 2020. Leaf resistance traits influence endophytic fungi colonization and community composition in a South American temperate rainforest. *Journal of Ecology* 108: 1019–1029.
- Grime JP. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, UK: J. Wiley.
- Grime JP, Hodgson J, Hunt R. 2007. *Comparative plant ecology. A functional approach to common British species*. London, UK: Castlepoint Press.
- Grman E, Allen J, Galloway E, McBride J, Bauer JT, Price PA. 2020. Inoculation with remnant prairie soils increased the growth of three native prairie legumes but not necessarily their associations with beneficial soil microbes. *Restoration Ecology* 28: S393–S399.
- Hacquard S, Schadt CW. 2015. Towards a holistic understanding of the beneficial interactions across the Populus microbiome. *New Phytologist* 205: 1424–1430.

- Hacquard S, Spaepen S, Garrido-Oter R, Schulze-Lefert P. 2017. Interplay between innate immunity and the plant microbiota. *Annual Review of Phytopathology* 55: 565–589.
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD *et al.* 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1: e1500052.
- Harrison JG, Griffin EA. 2020. The diversity and distribution of endophytes across biomes, plant phylogeny and host tissues: how far have we come and where do we go from here? *Environmental Microbiology* 22: 2107–2123.
- Haskins KE, Gehring CA. 2005. Evidence for mutualist limitation: the impacts of conspecific density on the mycorrhizal inoculum potential of woodland soils. *Oecologia* 145: 123–131.
- van der Heide T, Angelini C, de Fouw J, Eklöf JS. 2021. Facultative mutualisms: a double-edged sword for foundation species in the face of anthropogenic global change. *Ecology and Evolution* 11: 29–44.
- Hawkes CV, Bull JJ, Lau JA. 2020. Symbiosis and stress: how plant microbiomes affect host evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 375: 20190590.
- Helgason T, Daniell TJ, Husband R, Fitter AH, Young JPW. 1998. Ploughing up the wood-wide web? *Nature* 394: 431.
- Hobbs RJ, Higgs E, Hall CM, Bridgewater P, Chapin FS, Ellis EC, Ewel JJ, Hallett LM, Harris J, Hulvey KB *et al.* 2014. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment* 12: 557–564.
- Honnay O, Jacquemyn H, Bossuyt B, Hermy M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist* 166: 723–736.
- Houlton BZ, Wang YP, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454: 327–334.
- Huang K, Xia J, Wang Y, Ahlström A, Chen J, Cook RB, Cui E, Fang Y, Fisher JB, Huntzinger DN *et al.* 2018. Enhanced peak growth of global vegetation and its key mechanisms. *Nature Ecology & Evolution* 2: 1897–1905.
- Hulme PE. 2008. Phenotypic plasticity and plant invasions: is it all jack? *Functional Ecology* 22: 3–7.
- Jacobson AP, Riggio J, Tait AM, Baillie JEM. 2019. Global areas of low human impact ('low impact areas') and fragmentation of the natural world. *Scientific Reports* 9: 14179.
- Jentsch A, White P. 2019. A theory of pulse dynamics and disturbance in ecology. *Ecology* 100: e02734.
- Johnson NC, Graham JH. 2013. The continuum concept remains a useful framework for studying mycorrhizal functioning. *Plant and Soil* 363: 411–419.
- Kandlikar GS, Johnson CA, Yan X, Kraft NJB, Levine JM. 2019. Winning and losing with microbes: how microbially mediated fitness differences influence plant diversity. *Ecology Letters* 22: 1178–1191.
- Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC. 2012. Intensive agriculture erodes  $\beta$ -diversity at large scales. *Ecology Letters* 15: 963–970.
- Kiesewetter KN, Afkhami ME. 2021. Microbiome-mediated effects of habitat fragmentation on native plant performance. *New Phytologist* 232: 1823–1838.
- Kiesewetter KN, Otano L, Afkhami ME. 2023. Fragmentation disrupts microbial effects on native plant community productivity. *Journal of Ecology* 111: 1292–1307.
- Klock MM, Barrett LG, Thrall PH, Harms KE. 2015. Host promiscuity in symbiont associations can influence exotic legume establishment and colonization of novel ranges. *Diversity and Distributions* 21: 1193–1203.
- Koide RT, Schreiner RP. 1992. Regulation of the vesicular-arbuscular mycorrhizal symbiosis. *Annual Review of Plant Physiology and Plant Molecular Biology* 43: 557–581.
- Lambers H, Teste FP. 2013. Interactions between arbuscular mycorrhizal and non-mycorrhizal plants: do non-mycorrhizal species at both extremes of nutrient availability play the same game? *Plant, Cell & Environment* 36: 1191–1195.
- Lekberg Y, Arnillas CA, Borer ET, Bullington LS, Fierer N, Kennedy PG, Leff JW, Luis AD, Seabloom EW, Henning JA. 2021. Nitrogen and phosphorus fertilization consistently favor pathogenic over mutualistic fungi in grassland soils. *Nature Communications* 12: 3484.
- Lemanceau P, Blouin M, Muller R, Moëgne-Loccoz Y. 2017. Let the core microbiota be functional. *Trends in Plant Science* 22: 583–595.
- Liang S, Guo H, McCormack ML, Qian Z, Huang K, Yang Y, Xi M, Qi X, Ou X, Liu Y *et al.* 2023. Positioning absorptive root respiration in the root economics space across woody and herbaceous species. *Journal of Ecology* 111: 2710–2720.
- Liu H, Li J, Carvalhais LC, Percy CD, Prakash Verma J, Schenk PM, Singh BK. 2021. Evidence for the plant recruitment of beneficial microbes to suppress soil-borne pathogens. *New Phytologist* 229: 2873–2885.
- Lü P-P, Zheng Y, Chen L, Ji N-N, Yao H, Maitra P, Hu H-W, Li X-C, Guo L-D. 2020. Irrigation and fertilization effects on arbuscular mycorrhizal fungi depend on growing season in a dryland maize agroecosystem. *Pedobiologia* 83: 150687.
- MacArthur RH. 1972. *Geographical ecology. Patterns in the distribution of species.* New York, NY, USA: Harper and Row.
- Makiola A, Holdaway RJ, Wood JR, Orwin KH, Glare TR, Dickie IA. 2022. Environmental and plant community drivers of plant pathogen composition and richness. *New Phytologist* 233: 496–504.
- Mandyam KG, Jumpponen A. 2015. Mutualism-parasitism paradigm synthesized from results of root-endophyte models. *Frontiers in Microbiology* 5: 776.
- Margulis L. 1991. Symbiosis as a source of evolutionary innovation: speciation and morphogenesis. In: Margulis L, Fester R, eds. *Symbiogenesis and symbiogenesis.* Cambridge, UK: MIT Press, 1–14.
- Marro N, Grilli G, Soteras F, Caccia M, Longo S, Cofré N, Borda V, Burni M, Janoušková M, Urceley C. 2022. The effects of arbuscular mycorrhizal fungal species and taxonomic groups on stressed and unstressed plants: a global meta-analysis. *New Phytologist* 235: 320–332.
- McKinney ML, Lockwood JL. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14: 450–453.
- Menge DN, Wolf AA, Funk JL. 2015. Diversity of nitrogen fixation strategies in Mediterranean legumes. *Nature Plants* 1: 15064.
- Menge DNL, Chazdon RL. 2016. Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. *New Phytologist* 209: 965–977.
- Menge DNL, Lichstein JW, Angeles-Perez G. 2014. Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. *Ecology* 95: 2236–2245.
- Mengistu AA. 2020. Endophytes: colonization, behaviour, and their role in defense mechanism. *International Journal of Microbiology* 2020: 1–8.
- Menzel A, Hempel S, Klotz S, Moora M, Pysek P, Rillig MC, Zobel M, Kuhn I. 2017. Mycorrhizal status helps explain invasion success of alien plant species. *Ecology* 98: 92–102.
- Mesny F, Hacquard S, Thomma BP. 2023. Co-evolution within the plant holobiont drives host performance. *EMBO Reports* 24: e57455.
- Moora M. 2014. Mycorrhizal traits and plant communities: perspectives for integration. *Journal of Vegetation Science* 25: 1126–1132.
- Moyano J, Rodriguez-Cabal MA, Nuñez MA. 2020. Highly invasive tree species are more dependent on mutualisms. *Ecology* 101: e02997.
- Nouri E, Surve R, Bapaume L, Stumpe M, Chen M, Zhang Y, Ruyter-Spira C, Bouwmeester H, Glauser G, Bruissin S *et al.* 2021. Phosphate suppression of arbuscular mycorrhizal symbiosis involves gibberellic acid signaling. *Plant and Cell Physiology* 62: 959–970.
- Nuske SJ, Fajardo A, Nuñez MA, Pauchard A, Wardle DA, Nilsson M-C, Kardol P, Smith JE, Peltzer DA, Moyano J *et al.* 2021. Soil biotic and abiotic effects on seedling growth exhibit context-dependent interactions: evidence from a multi-country experiment on *Pinus contorta* invasion. *New Phytologist* 232: 303–317.
- Oldroyd GED, Leyser O. 2020. A plant's diet, surviving in a variable nutrient environment. *Science* 368: eaba0196.
- Pérez-de-Luque A, Tille S, Johnson I, Pascual-Pardo D, Ton J, Cameron DD. 2017. The interactive effects of arbuscular mycorrhiza and plant growth-promoting rhizobacteria synergistically enhance host plant defences against pathogens. *Scientific Reports* 7: 16409.
- Pither J, Pickles BJ, Simard SW, Ordóñez A, Williams JW. 2018. Below-ground biotic interactions moderated the postglacial range dynamics of trees. *New Phytologist* 220: 1148–1160.
- Pohlman CL, Nicotra AB, Murray BR. 2005. Geographic range size, seedling ecophysiology and phenotypic plasticity in Australian *Acacia* species. *Journal of Biogeography* 32: 341–351.
- Pozo MJ, Lopez-Raez JA, Azcon-Aguilar C, García-Garrido JM. 2015. Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses. *New Phytologist* 205: 1431–1436.
- Preston FW. 1948. The commonness, and rarity, of species. *Ecology* 29: 254–283.
- Questad EJ, Foster BL. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters* 11: 717–726.

- Ramirez KS, Snoek LB, Koorem K, Geisen S, Bloem LJ, ten Hooven F, Kostenko O, Krigas N, Manrubia M, Caković D *et al.* 2019. Range-expansion effects on the belowground plant microbiome. *Nature Ecology & Evolution* 3: 604–611.
- Raven JA, Lambers H, Smith SE, Westoby M. 2018. Costs of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. *New Phytologist* 217: 1420–1427.
- Reynolds HL, Mittelbach GG, Darcy-Hall TL, Houseman GR, Gross KL. 2007. No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *Journal of Ecology* 95: 723–733.
- Rilling JI, Acuña JJ, Nannipieri P, Cassan F, Maruyama F, Jorquera MA. 2019. Current opinion and perspectives on the methods for tracking and monitoring plant growth-promoting bacteria. *Soil Biology and Biochemistry* 130: 205–219.
- Sabatini FM, Lenoir J, Hattab T, Arnst EA, Chytrý M, Dengler J, De Ruffray P, Hennekens SM, Jandt U, Jansen F *et al.* 2021. sPlotOpen – an environmentally balanced, open-access, global dataset of vegetation plots. *Global Ecology and Biogeography* 30: 1740–1764.
- Schittko C, Bernard-Verdier M, Heger T, Buchholz S, Kowarik I, von der Lippe M, Seitz B, Joshi J, Jeschke JM. 2020. A multidimensional framework for measuring biotic novelty: How novel is a community? *Global Change Biology* 26: 4401–4417.
- Schneider HM. 2022. Characterization, costs, cues and future perspectives of phenotypic plasticity. *Annals of Botany* 130: 131–148.
- Semmartin M, Omacini M, Gundel PE, Hernandez-Agramonte IM. 2015. Broad-scale variation of fungal-endophyte incidence in temperate grasses. *Journal of Ecology* 103: 184–190.
- Shemesh H, Boaz BE, Millar CI, Bruns TD. 2020. Symbiotic interactions above treeline of long-lived pines: mycorrhizal advantage of limber pine (*Pinus flexilis*) over Great Basin bristlecone pine (*Pinus longaeva*) at the seedling stage. *Journal of Ecology* 108: 908–916.
- Sikes BA, Cottenie K, Klironomos JN. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *Journal of Ecology* 97: 1274–1280.
- Simonsen AK, Dinnage R, Barrett LG, Prober SM, Thrall PH. 2017. Symbiosis limits establishment of legumes outside their native range at a global scale. *Nature Communications* 8: 14790.
- Singh BK, Delgado-Baquerizo M, Egidi E, Guirado E, Leach JE, Liu H, Trivedi P. 2023. Climate change impacts on plant pathogens, food security and paths forward. *Nature Reviews Microbiology* 21: 640–656.
- Sirami C, Caplat P, Popy S, Clamens A, Arlettaz R, Jiguet F, Brotons L, Martin J-L. 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography* 26: 385–394.
- Slobotkin LB, Sanders HL. 1969. On the contributions of environmental predictability to species diversity. *Brookhaven Symposia in Biology* 22: 82–95.
- Smith FA, Smith SE. 2015. How harmonious are arbuscular mycorrhizal symbioses? Inconsistent concepts reflect different mindsets as well as results. *New Phytologist* 205: 1381–1384.
- Soudzilovskaia NA, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett MC, Gomes SIF, Merckx V, Tedersoo L. 2020. FungalRoot: global online database of plant mycorrhizal associations. *New Phytologist* 227: 955–966.
- Staudé IR, Pereira HM, Daskalova GN, Bernhardt-Römermann M, Diekmann M, Pauli H, Van Calster H, Vellend M, Bjorkman AD, Brunet J *et al.* 2022. Directional turnover towards larger-ranged plants over time and across habitats. *Ecology Letters* 25: 466–482.
- Taylor BN, Chazdon RL, Menge DNL. 2019. Successional dynamics of nitrogen fixation and forest growth in regenerating Costa Rican rainforests. *Ecology* 100: e02637.
- Tedersoo L, Bahram M, Zobel M. 2020. How mycorrhizal associations drive plant population and community biology. *Science* 367: 867.
- Theis KR, Dheilly NM, Klassen JL, Brucker RM, Baines JF, Bosch TCG, Cryan JF, Gilbert SF, Goodnight CJ, Lloyd EA *et al.* 2016. Getting the hologenome concept right: an eco-evolutionary framework for hosts and their microbiomes. *mSystems* 1: e00028-16.
- Thrall PH, Hochberg ME, Burdon JJ, Bever JD. 2007. Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution* 22: 120–126.
- Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgely GF, Paterson J, Schurr FM *et al.* 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 137–152.
- Treseder KK, Allen EB, Egerton-Warburton LM, Hart MM, Klironomos JN, Maherali H, Tedersoo L, Wurzburger N. 2018. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: a trait-based predictive framework. *Journal of Ecology* 106: 480–489.
- Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK. 2020. Plant–microbiome interactions: from community assembly to plant health. *Nature Reviews Microbiology* 18: 607–621.
- Van Kleunen M, Fischer M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* 166: 49–60.
- Vela Díaz DM, Blundo C, Cayola L, Fuentes AF, Malizia LR, Myers JA. 2020. Untangling the importance of niche breadth and niche position as drivers of tree species abundance and occupancy across biogeographic regions. *Global Ecology and Biogeography* 29: 1542–1553.
- Veresoglou SD, Barto EK, Meneses G, Rillig MC. 2013. Fertilization affects severity of disease caused by fungal plant pathogens. *Plant Pathology* 62: 961–969.
- Veresoglou SD, Rillig MC. 2012. Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. *Biology Letters* 8: 214–217.
- Větrovský T, Kohout P, Kopecký M, Machac A, Man M, Bahnmann BD, Brabcová V, Choi J, Meszárosová L, Human ZR *et al.* 2019. A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nature Communications* 10: 5142.
- Vitousek P. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861–1902.
- Vlk L, Tedersoo L, Antl T, Větrovský T, Abarenkov K, Pergl J, Albrechtová J, Vosátka M, Baldrian P, Pyšek P *et al.* 2020. Alien ectomycorrhizal plants differ in their ability to interact with co-introduced and native ectomycorrhizal fungi in novel sites. *The ISME Journal* 14: 2336–2346.
- Wan X, Chen X, Huang Z, Chen HYH. 2021. Global soil microbial biomass decreases with aridity and land-use intensification. *Global Ecology and Biogeography* 30: 1056–1069.
- Watson James EM, Shanahan Danielle F, Di Marco M, Allan J, Laurance William F, Sanderson Eric W, Mackey B, Venter O. 2016. Catastrophic declines in wilderness areas undermine global environment targets. *Current Biology* 26: 2929–2934.
- Weber A, Karst J, Gilbert B, Kimmins JP. 2005. Thuja plicata exclusion in ectomycorrhiza-dominated forests: testing the role of inoculum potential of arbuscular mycorrhizal fungi. *Oecologia* 143: 148–156.
- Weber SE, Diez JM, Andrews LV, Goulden ML, Aronson EL, Allen MF. 2019. Responses of arbuscular mycorrhizal fungi to multiple coinciding global change drivers. *Fungal Ecology* 40: 62–71.
- Wernegreen JJ, Wheeler DE. 2009. Remaining flexible in old alliances: functional plasticity in constrained mutualisms. *DNA and Cell Biology* 28: 371–382.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- Williams JL, Kendall BE, Levine JM. 2016. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. *Science* 353: 482–485.
- Yang X, Chen J, Shen Y, Dong F, Chen J. 2020. Global negative effects of livestock grazing on arbuscular mycorrhizas: a meta-analysis. *The Science of the Total Environment* 708: 134553.
- Zeleny D, Chytrý M. 2019. Ecological specialization indices for species of the Czech flora. *Preslia* 91: 93–116.
- Zhan C, Matsumoto H, Liu Y, Wang M. 2022. Pathways to engineering the phyllosphere microbiome for sustainable crop production. *Nature Food* 3: 997–1004.
- Zheng Z, Ma PF, Li J, Ren LF, Bai WM, Tian QY, Sun W, Zhang WH. 2018. Arbuscular mycorrhizal fungal communities associated with two dominant species differ in their responses to long-term nitrogen addition in temperate grasslands. *Functional Ecology* 32: 1575–1588.
- Zhu Z, Piao S, Myneni RB, Huang M, Zeng Z, Canadell JG, Ciais P, Sitch S, Friedlingstein P, Arneeth A *et al.* 2016. Greening of the earth and its drivers. *Nature Climate Change* 6: 791–795.

Zobel M, Moora M, Pärtel M, Semchenko M, Tedersoo L, Öpik M, Davison J. 2023. The multiscale feedback theory of biodiversity. *Trends in Ecology & Evolution* 38: 171–182.

### Supporting Information

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

**Fig. S1** Mycorrhizal flexibility of plant species with the highest abundance and occupancy in herbaceous vegetation plots in the sPlotOpen database.

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