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Research review

The root microlandscape of arbuscular mycorrhizal fungi

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Summary

Understanding the drivers of assemblages of arbuscular mycorrhizal fungi (AMF) is essential to leverage the benefits of AMF for plant growth and health. Arbuscular mycorrhizal fungi are heterogeneously distributed in space even at small scale. We review the role of plant distribution in driving AMF assemblages (the passenger hypothesis), using a transposition of the conceptual framework of landscape ecology. Because rooting systems correspond to habitat patches with limited carrying capacity that differ in quality due to host-preference effects, we suggest considering plant communities as mosaics of AMF microhabitats. We review how predictions from landscape ecology apply to plant community effects on AMF, and the existing evidence that tests these predictions. Although many studies have been conducted on the effect of plant compositional heterogeneity on AMF assemblages, they mostly focused on the effect of plant richness, while only a few investigated the effect of configurational heterogeneity, plant connectivity or plant community temporal dynamics. We propose key predictions and future prospects to fill these gaps. Considering plant communities as landscapes extends the passenger hypothesis by including a spatially explicit dimension and its associated ecological processes and may help understand and manipulate AMF assemblages at small spatial scales.

Introduction

Mycorrhizal fungi are a major component of soil diversity in most terrestrial ecosystems and have a tremendous impact on plant biology, productivity, and overall nutrient cycling (Van der Heijden *et al.*, 2006; Tedersoo *et al.*, 2020). Among the different types of mycorrhizal symbioses with plants, the most frequent by far is with arbuscular mycorrhizal fungi (AMF) that colonize *c.* 80% of all terrestrial plants and > 95% of plant families (Smith & Read, 2008). Arbuscular mycorrhizal fungi colonize root cortical cells and develop a dense extra-radical mycelium that forms an extensive network in the soil. This symbiosis not only enables the fungus to acquire carbon and the host plant to acquire phosphorus and other nutrients beyond the root depletion zone (Averill *et al.*, 2019), but also to resist environmental stresses (Vannier *et al.*, 2015). A better understanding is needed of how manipulating AMF communities associated with plants is a key issue in plant production for which more environmental-friendly practices are required to reduce the negative impacts of high nutrients and pesticide inputs in fields. The distribution of AMF in the soil is highly heterogeneous in space and over time even at

a small scale (Bahram *et al.*, 2015). Therefore, the AMF community composition is often interpreted as being stochastic or idiosyncratic (Dumbrell *et al.*, 2010a,b; Lekberg *et al.*, 2012; Encinas-Viso *et al.*, 2016; Kokkoris *et al.*, 2020). Part of this heterogeneity is due to small-scale microedaphic and climatic conditions (Davison *et al.*, 2015) or localized disturbances (Jiang *et al.*, 2020). Vegetation can also play an important role at small spatial scale where the abiotic environment is assumed to be homogeneous (Vályi *et al.*, 2016). Although AMF are often perceived as generalists, a ‘host preference’ has been demonstrated among coexisting plants (Vandenkoornhuys *et al.*, 2003) resulting from the host-imposed AMF species filtering (Fig. 1a,b). At a given location, the reservoir of AMF propagules is a consequence of the living plants but also of former living plants (*soil legacy effect*, Bitttebiere *et al.*, 2020). Because of intimate interactions between AMF and plants, the spatial distribution of AMF may mirror that of plant roots (*passenger hypothesis*, Hart *et al.*, 2001). Host–plant mixtures are likely influencing AMF assembly mechanisms through the spatial and temporal heterogeneity of niche availability and AMF dispersal between host plants.

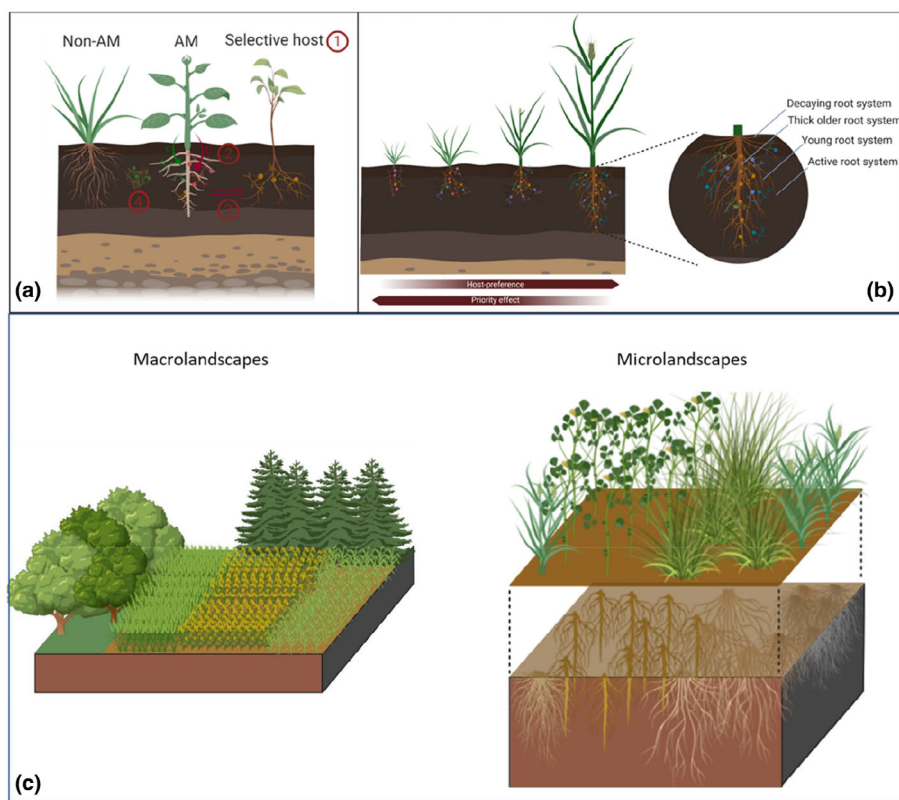


Fig. 1 Plant landscapes for arbuscular mycorrhizal fungi (AMF). (a) Ecological mechanisms involved in the host-preference effect at the individual plant level (1. genetic drivers of AMF colonization, 2. reward process through allocation of carbohydrates by the plant, 3. plant root architecture, 4. AMF in decomposing roots), (b) AMF dynamics along plant development. The priority effect decreases while the host-preference effect increases over time. The plant rooting system represents a habitat with a limited carrying capacity due to the limited area available for colonization. It includes marked microheterogeneity in habitat quality due to root activity and morphology. (c) Analogy between macrolandscape and floristic landscape structure – landscapes are made of different types of patches – Floristic landscapes are generally described using aboveground plant distribution while floristic landscapes for AMF are made of the belowground rooting systems. Figure created with [BioRender.com](https://www.biorender.com).

Landscape ecology provides a rich conceptual framework to understand the relationships between habitat spatial patterns and ecological processes. Originally developed for macroorganisms, landscape ecology analyzes ‘landscapes’ as mosaics of different habitat patches (Table 1; Fig. 1c). This concept assumes that patches have limiting carrying capacities and are related to each other through ecological processes that operate at large spatial scales and affect species distribution. By analogy, plant communities are made up of many plant rooting systems, each of which can be colonized on a very small spatial scale by a mixture of AMF species. These rooting systems display (1) a limiting carrying capacity to harbor AMF, (2) specific habitat characteristics, and (3), are connected by dispersal fluxes of AMF among the roots (Fig. 1a). Indeed, once AMF colonize roots, there is intense competition among AMF species for root space especially when they undergo strong intra-radical growth (Cano & Bago, 2005; Engelman *et al.*, 2014). Consequently, AMF species that primarily randomly colonize a seedling are likely to influence subsequent assemblages (*Priority effect* Fig. 1b), as demonstrated experimentally by Vierheilig (2004) and Werner & Kiers (2015). Second, the host plant may regulate colonization using mechanisms that can be both passive (e.g. morphology and architecture of the roots, Eissenstat *et al.*, 2015; Liu *et al.*, 2015) and active. Active mechanisms include the production of exudates (Sasse *et al.*, 2018), which can vary over the course of plant development and consequently affect the plant microbiome (Chaparro *et al.*, 2014) and cause selective allocation of photosynthates to specific AMF depending on their level of cooperation (Bever *et al.*, 2009; Kiers *et al.*, 2011) (Fig. 1a). There is also high complementarity between roots and fungi in multiple

functions including nutrition and protection against pathogens that may affect AMF recruitment (Sikes *et al.*, 2009). Thus host–plant regulation and AMF–AMF interactions can result in temporal changes in assemblages in a given plant with both inter- and intra-annual change (Vandenkoornhuys *et al.*, 2003; Santos-Gonzalez *et al.*, 2007; Bennett *et al.*, 2013). As a result, plant rooting systems represent AMF microhabitats of different types depending on both host identity and on functional traits related to root morphology, growth and phenology, that may vary in space and over time, hence shaping AMF distribution. Lastly, AMF spread among plants within a community by developing mycelium that directly interconnects plant rooting systems, the transmission of propagules through contact between roots, or through colonized root pieces and spores (Smith & Read, 2008; Fig. 1a). Plant landscapes can be described using the same features as classical landscapes (i.e. spatial patterns of interacting habitat patches, see Table 1 forming a mosaic), they can be compared to ‘small-scale’ landscapes for AMF formed by rooting systems, that can be described using estimated plant distribution based on aboveground cover (Fig. 1c). The similarity between aboveground and belowground description of plant species distribution is likely to depend on the extent of root intermingling between neighbor plants. Nevertheless, the analogy to landscapes makes it possible to investigate whether key concepts of landscape ecology apply at this small scale.

A plant community is a combination of individual plants of different taxonomic and functional identities that influence the composition of fungal microhabitats. Plants are not arranged randomly but rather display a range of spatial patterns, from

Table 1 Main definitions of macrolandscapes and their transposition to floristic landscape and definitions of biodiversity response to landscape modifications.

	Landscape for macroorganisms	Floristic landscape for arbuscular mycorrhizal fungi (AMF)
Habitat patch	A landscape element that forms part of or the entire species habitat. Patches that harbor populations of species and communities are subject to the arrival of individuals/species, biotic interactions, environmental stochasticity (Leibold <i>et al.</i> , 2004). Patch categories can be type of land-use, landcover or ecological habitats. Patch boundaries are delimited by a change in patch type.	A habitat formed by plants that support AMF growth. Patch categories can be the rooting system of individuals (e.g. genotypes), plant species, plant functional guilds (e.g. leguminous vs Graminean), plant ecological groups (eutrophic vs oligotrophic) or any other category of ecological interest (e.g. invasive vs native) that are relevant to describe the mosaic of plants cover.
Landscape	A physical space defined spatially and temporally. A landscape comprises a mosaic of patches of different habitat types that are interrelated through a range of ecological processes (e.g. abiotic and biotic fluxes) (Fig. 1c). Variables to describe landscape structure can be measured at the patch level (see definitions of landscape structural connectivity, habitat amount, habitat fragmentation <i>per se</i>) or at the mosaic level (see definitions of landscape functional heterogeneity, connectivity, temporal landscape variability). A landscape can be described as a mosaic of habitats patches (<i>landscape-mosaic model</i> , Wiens, 1995), as a binary structure of habitat vs nonhabitat patches (<i>patch-matrix model</i> , Wiens, 1997; Brudvig <i>et al.</i> , 2017) if the effect of landscape mosaic is secondary (Fig. 2a), or as a continuum of environmental variables (McGarigal & Cushman, 2005).	A plant community comprised of a mosaic of individual plants/species/plant types that can be dynamic over time. A plant community can be described at the individual level (the size of an individual, for instance), at the species level (the plant cover, for instance) or at the plant community level (plant richness, for instance). Landscape can correspond to either aboveground or to belowground plant mosaic (Fig. 1c). A floristic landscape could be seen either as a mosaic of different host plants (<i>landscape-mosaic model</i>), or as a set of host–nonhost plants (<i>patch-matrix model</i>).
Landscape mosaic	A mosaic of delimited patches of different habitat types within a landscape.	A mosaic of plant patches resulting from aggregated plant growth or plant rooting system of one/several individuals. In most studies, plant mosaic is approximated from the aboveground cover, instead of the belowground one which is the effective landscape that influences AMF distribution.
Landscape heterogeneity	The composition (nature and diversity) and the configuration (spatial arrangement) of the different habitat- patches that form the landscape mosaic (Fahrig <i>et al.</i> , 2011; Fig. 2c).	The composition of plants and their configuration in space. Plant categories can be determined through different ways (see habitat patch definition). Patch boundaries can be well delimited if plant individual/species are segregated in space or blurred if plant individuals/species overlap spatially.
Landscape connectivity	Connectivity is the measure of the set of landscape elements in the mosaic that facilitate or impede the movement of species (Taylor <i>et al.</i> , 1993; Fig. 3a). Connectivity can be structural (i.e. involving patches of the only habitat concerned) and measured as the physical distance between patches (e.g. inverse of habitat isolation) and/or size patch; or connectivity can be functional (i.e. integrating species dispersal response to the landscape-mosaic and/or patch quality). Functional connectivity is based for instance on the difference in permeability (i.e. ability of the habitat type to promote species dispersal, the contrary is resistance) that allows a given species to be dispersed among different habitat types. Structural connectivity thus depends on the characteristics and distribution of the habitat patches, while functional connectivity is related to landscape-mosaic heterogeneity. Potential connectivity is measured through proxies of dispersal, whereas actual connectivity is measured with surveys of real dispersal movements (e.g. individual tracking or genetics).	The effect of plant mosaic on AMF dispersal among plants. Structural connectivity can be related to the distance between target host plants, while functional connectivity can be related to the distance of dispersal of AMF species and their ability to transfer through the plant mosaic depending on the different types of plants constituting the mosaic. Functional connectivity assumes that other plants of the mosaic than the preferential host plants can be alternative hosts or barriers to AMF dispersal, and therefore, influence the ability of AMF to transfer from one host–plant patch to another.
Landscape temporal variability	Temporal changes in landscape structure due to natural succession processes, natural disturbances and/or human activities (Fig. 2c).	Temporal changes in plant mosaic structure due to plant biological traits (e.g. life span, lateral growth), plant–plant interactions (e.g. competition, facilitation), small-scale external disturbances due to biotic (e.g. animal predatory) or abiotic (e.g. local environmental stresses) factors. It can be described at different time scales (intra-annual, inter-annual, decades).
Habitat amount	Amount of habitat of a given type in the landscape mosaic.	Abundance per plant species or per other plant categories (see definition of habitat) in the floristic landscape.

Table 1 (Continued)

	Landscape for macroorganisms	Floristic landscape for arbuscular mycorrhizal fungi (AMF)
Habitat fragmentation <i>per se</i>	Distribution of habitat patches in the landscape for a given habitat amount. It is closely linked to the habitat isolation concept which focuses only on the distance part among patch types. High fragmentation <i>per se</i> corresponds to numerous small habitat patches while low fragmentation <i>per se</i> corresponds to fewer big habitat patches (Fahrig, 2003).	Distribution of plant patches of a given species within the community. High fragmentation <i>per se</i> should correspond to plant species that are distributed sparsely in the community, while low fragmentation <i>per se</i> should correspond to highly aggregated plant species forming large and distant patches. Habitat isolation would correspond to the distance between habitat patches belonging to the same category.
Biodiversity response to landscape structure	Response can be detected at the patch level (local community – Alpha diversity) or at the landscape level (landscape assemblage – Gamma diversity), or as the difference among patches (convergence or divergence among local communities – Beta diversity). Biodiversity response can be assessed with respect to taxonomy (species composition), function (species traits, species functional guilds) or ecology (species ecological traits). The response is the result of different processes including species dispersal and species establishment within patches.	Response can be detected at the individual level (AMF associated with one plant rooting system), at the patch level (AMF associated with several individuals, constituting the same patch – which samples are potentially pooled), or at the population level (several individuals sampled across the floristic landscape), or as the difference among local communities (individual or patch).
Dispersal	Ecological process linked to the movement of individuals from their natal patch to another area. Hence, dispersal can be split into three consecutive steps, departure from the initial patch, movement between the natal and the final patch, and arrival at the final patch. All the steps involved in dispersal are largely determined by the species' biological traits (Ronce, 2007).	Dispersal in AMF mostly involve hyphae development, hyphae anastomosis with other hyphal networks, transmission through root contacts, spore or hyphae fragments dispersal through small-size vectors (collembola, worms) (Smith & Read, 2008).
Colonization credit	Delayed colonization of populations/species in a given patch in response to a change in landscape structure. The delay is linked to the duration of dispersal (i.e. the time between departure and the arrival stages) and will last until the new communities reach equilibrium (Kuussaari <i>et al.</i> , 2009; Jackson & Sax, 2010).	Delayed colonization of plant rooting systems of a given plant species, that could be due to dispersal duration including AMF transfer but also ability to get through the plant defense mechanisms and colonize the root endosphere.
Extinction debt	Delayed extinction of populations/species in a given patch in response to a change in landscape structure. The delay is linked to efficient establishment strategies that enable organisms to survive and reproduce in a given patch even if no more individuals arrive occurs (Jackson & Sax, 2010).	Delayed extinction of AMF associated with plant rooting systems of a given plant species. It could be due to a strong ability to develop locally through hyphae growth, and a balanced cooperation between AMF and plant individuals resulting from plant rewarding process to AMF (Kiers <i>et al.</i> , 2011).

sparingly distributed to strongly aggregated (Law & Dieckmann, 2000; Fig. 1c), as a result of plant–plant interactions, small-scale plant dispersal and environmental heterogeneity (Herben & Hara, 2003). If each plant corresponds to a potential habitat niche for microorganisms, plant composition and spatial arrangement will consequently influence the vertical and horizontal distribution of root fragments and hence the distribution of AMF habitats and their interrelations (Fig. 1c). The main assumptions based on the conceptual framework of landscape ecology are listed in Table 2. We expect that (1) root landscape structure influences species patterns through the influence of floristic landscape heterogeneity on dispersal. The composition and configuration of heterogeneous landscapes (Table 1) are associated with higher diversity due to increased habitat diversity and less isolated habitat patches while homogeneous landscapes are hypothesized to be linked with lower diversity and the selection of a given set of species; (2) habitat fragmentation *per se* (Table 1) selects for species able to disperse despite isolated habitat patches. Less isolated habitat patches are expected to reduce species biodiversity by increasing species fluxes among patches; (3) temporal changes in landscape structure (Table 1) may affect species composition and diversity as a result of delayed response due to the duration of dispersal across dynamic mosaic and patch colonization processes. We explored existing evidence for the effects of plant composition, configuration

and connectivity in space and over time on microorganisms, using AMF communities (Fig. 2) in order to test these assumptions. Due to the impact of AMF on plant growth and development, it is virtually impossible to disentangle the effect of plants on AMF from the feedback effect of AMF on plant distribution (i.e. *the driver hypothesis*, Hart *et al.*, 2001). In the following, to investigate the consequences of these manipulations for the distribution of AMF in soil and roots, we, therefore, mainly focus on experiments that manipulate plant composition and configuration (i.e. we excluded observational studies because plant distribution and environmental homogeneity cannot be decoupled). We also favored studies that analyze AMF assemblages using amplicon mass-sequencing so that AMF community composition is well described (i.e. except when no other studies were available, we did not include studies that account for plant community effects on AMF based on spore counts and identification).

Plant compositional heterogeneity of the microlandscape

Landscape composition is usually investigated through habitat types, using metrics of habitat richness, evenness or relative cover (Table 2; Fig. 2c). Higher compositional heterogeneity is assumed to influence species composition by influencing the pool of species

Table 2 From macrolandscapes to microlandscapes.

	Ecological processes involved	Available metrics	Biodiversity response to increased values	Analogy to plant- arbuscular mycorrhizal fungi (AMF) relationships	Applications for AMF manipulation in plant production
Compositional heterogeneity	Types of ecological niche available Sources of propagule/individuals available for dispersal Access to available resources (for animals, for example niche supplementation or complementation; Dunning <i>et al.</i> , 1992)	Habitat type richness Habitat type evenness	Increase in species richness until a certain threshold is reached, followed by decrease in species richness due to the indirect effect of changes in configuration (<i>Intermediate heterogeneity hypothesis</i> , Fahrig <i>et al.</i> , 2011) Changes in species composition	Set of different plant individuals/species, with potentially varying abundance within a community	Mixed-species and or mixed-cultivar crops Coexistence between weeds and crop plants Grasslands or forests with high species richness
Configurational heterogeneity	Dispersal limitations (Tschamtko <i>et al.</i> , 2012) Patch carrying capacity Edge effect among patches of different types (Fagan <i>et al.</i> , 1999; Ries <i>et al.</i> , 2004)	Mean distance between patches of similar type Mean patch size Proportion of interfaces between different types of habitat (Cushman <i>et al.</i> , 2008)	Increase in species richness until a certain threshold is reached, followed by decrease in species richness (<i>Intermediate heterogeneity hypothesis</i> , Fahrig <i>et al.</i> , 2011) Modulated by species traits Species spillover from one habitat to another habitat located nearby	Set of different sized patches of different individual plants/species ^a	Inter-rank cropping Spatial arrangement of plants in mixture (e.g. permaculture techniques)
Habitat amount	Limitation/availability of resources for species establishment and development Carrying capacity	Habitat cover	Increase in species richness (<i>Habitat amount hypothesis</i> ; Fahrig, 2013) Coexistence of species with different strategies	Abundance of a given plant genotype/species (cover percentage, biomass, ...)	Sowing/Planting density
Habitat isolation Habitat low connectivity	Limited dispersal and decrease in the flow of species among patches	Distance between patches (physical or functional)	Decrease in species richness (<i>Equilibrium theory of island biogeography</i> , MacArthur & Wilson, 1967), dependent on patch size. Selection of species with high dispersal abilities	Isolation/ low connectivity among plants of similar types Connectivity can be calculated taking into account the whole plant mosaic or only the host-plant patches	Sowing/Planting pattern of a given plant
Landscape temporal variability	Timing for species establishment and population growth rate Duration and timing of dispersal processes	Habitat turnover rate Past landscape structure	Increase in species richness up to a certain threshold, followed by decrease in richness resulting in marked instability (<i>Metacommunity theory</i> , Leibold <i>et al.</i> , 2004) Delayed effect on local community structure (diversity, composition) for a given patch (e.g. composition is better predicted by past landscape structure that current one, Jackson & Sax, 2010)	Change in plant mosaic over time due to intra-annual change (age of individual plant, early vs late species), inter-annual change (plants with different life spans), inter-decadal changes (succession processes) Change in plants as a response to environmental changes Plant-plant interactions	Mixtures of plants of different ages (e.g. particular management of forest stands, perennial crops) Mixtures of species with different life spans (e.g. permaculture techniques) Natural short-scale disturbances in ecosystems (e.g. grazed grasslands) Choice of inter cropping species Crop rotation

^aIn this table, habitat type can be replaced by land use, land cover, or by any habitat of ecological interest; species can be replaced by functional guilds (e.g. leguminous vs Poaceae) or ecological groups (eutrophic vs oligotrophic) or any other category of ecological interest (e.g. invasive vs native species).

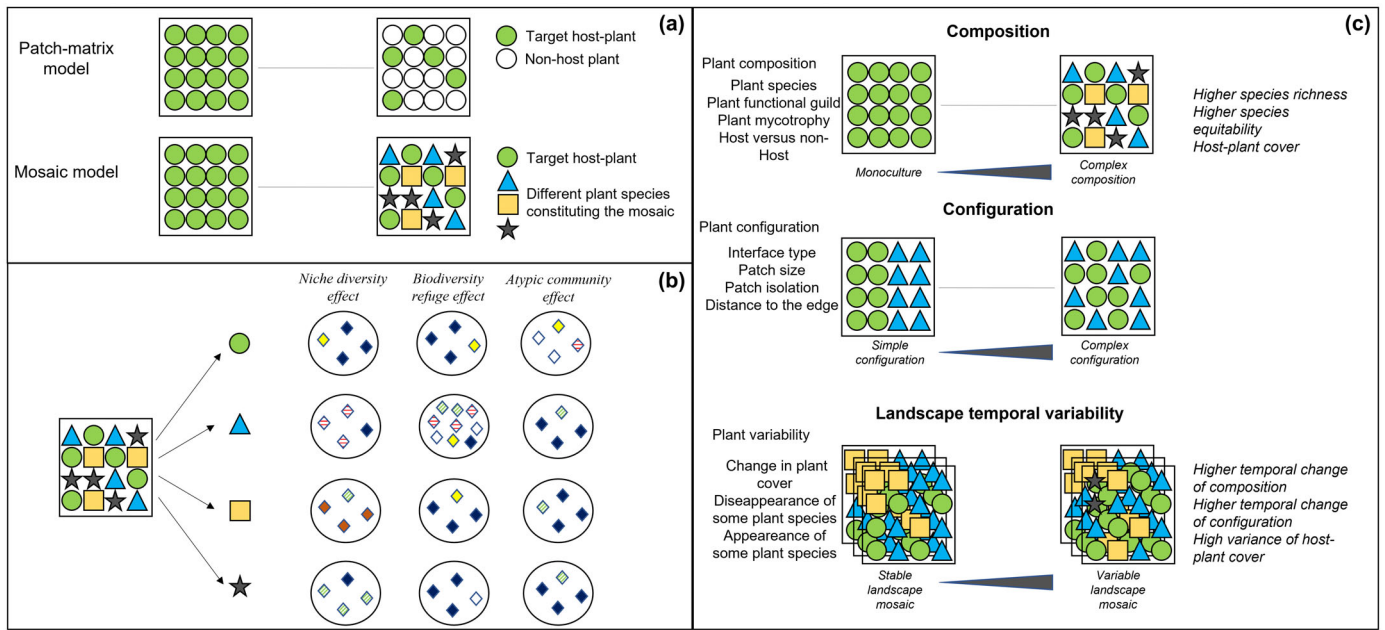


Fig. 2 Landscape concepts applied to plant communities. (a) Presentation of the two conceptual models of landscapes – the patch-matrix model considering habitat vs nonhabitat binary distribution (e.g. host plant vs nonhost plants) and the landscape-mosaic model considering a landscape as a mosaic of different habitat types whose characteristics affect target habitat assemblages (e.g. a mosaic of different plants for a floristic microlandscape); (b) Conceptual models to understand the relationships between landscapes comprising a large number of land-use types – here plant species, and assumed high species richness at the landscape level – here arbuscular mycorrhizal fungi richness – in all cases, we find the same richness but resulting from three different processes – the niche-diversity effect, the biodiversity-refuge effect, and the atypic-community effect; (c) Spatial heterogeneity and temporal variability of plant landscapes. Two components of spatial heterogeneity – composition and configuration – are considered. Description of landscape components and of variables at the landscape-mosaic and patch level. Different colored geometrical shapes represent different plant species distributed within a plant community. Different colored diamond symbols correspond to the different microbial species associated with each plant.

available for dispersal within the landscape and species that may depend on several habitats during their life cycle (Tscharrntke *et al.*, 2012; Table 2). Higher habitat type richness is hypothesized to support higher species richness due to a larger number of ecological niches (Allouche *et al.*, 2012; Fig. 2b), but this relationship is assumed to be true only in the case of intermediate degrees of habitat richness because of the induced decrease in patch area (*intermediate heterogeneity hypothesis*, Fahrig *et al.*, 2011). When transposed to floristic landscapes, up to now, the effect of plant community composition has mostly been studied through the effect of plant species richness. If transposed to plant communities/AMF relationships, rich plant communities may increase AMF diversity because (1) rich plant communities are more likely to include a few species that strongly differ in their ability to support particular AMF species compared to the other plant species (increase in niche specificity), (2) rich communities provide a wider range of root types to support AMF growth throughout the growing season (i.e. increase in niche diversity) (Fig. 2b). One of the first pieces of evidence for this positive effect was provided by Burrows & Pfleger (2002). The authors analyzed AMF diversity along a gradient of plant diversity, and controlled for a species identity effect by shuffling species composition within each diversity treatment. Hiiesalu *et al.* (2014) demonstrated that the positive effect of plant diversity on AMF richness, which was similar in bulk soil, was stronger when the identity of the roots rather

than shoots was used to measure plant diversity, suggesting the importance of the belowground landscape of roots. Whether this root diversity effect is related to a change in AMF dispersal due to roots identity itself or to an indirect effect on environmental microheterogeneity remains to be investigated. One key difference from usual landscape effects is the relationship with plant biomass: species-rich communities may increase plant productivity and, therefore, provide larger amounts of roots to colonize. The few studies that have taken plant biomass into account demonstrated that the positive impact of plant species richness on AMF diversity was independent of productivity (De Deyn *et al.*, 2011), or was sometimes even negatively correlated with productivity (Hedlund *et al.*, 2003; Hiiesalu *et al.*, 2014), suggesting that plant–AMF effects are more likely to be related to niche composition than to habitat availability.

Plant community composition is likely to determine AMF assemblages resulting from the observed preferential association of plants with a given AMF community. First, the plant composition effect was investigated by focusing on the abundance of a particular species within the plant community (i.e. the amount of habitat of a given type; Table 2). For instance, increased abundance of invasive plant species has been shown to affect AMF abundance in the soil and to result in less fungal colonization of native plant roots (Stinson *et al.*, 2006; Callaway *et al.*, 2008; Wilson *et al.*, 2012). It may also change AMF composition and diversity in both roots of

the invasive plant and of the neighboring indigenous species (Mummey & Rillig, 2006; Barto *et al.*, 2011). This effect was suggested to be the result of plant–plant competition and/or of the nonmycorrhizal status of the invasive plants used in the studies (Bunn *et al.*, 2015). To disentangle these effects and extrapolate the results to noninvasive plants, the impact of the identity of neighboring plants on a focal plant microbiota was assessed in detail in experimental conditions. Using a plant–matrix design, Hausmann & Hawkes (2010) demonstrated that the identity of neighboring plants influenced a focal plant species with synergistic effects (i.e. the community based on the initial pool of both species), controlling effects (i.e. converting the community of the focal plant into the community of the neighbors) or neutral effects (i.e. the AMF community remained invariant across treatments). While this study demonstrated a strong plant identity effect, the resulting consequences in multispecies plant neighborhoods are difficult to predict because of potentially opposing effects among plant species on the AMF community. In multispecies experimental setups, the composition of the plant neighborhood (i.e. the percentage cover of plant species) affected AMF composition at a scale of a few tens of centimeters in both roots (De Deyn *et al.*, 2011; Bittebiere *et al.*, 2020) and soil (Vannier *et al.*, 2020). The effect of neighbor plant species on the focal plant microbiota was predicted by their functional traits (legumes or C4 grasses in Burrows & Pflieger, 2002; root functional traits in Mony *et al.*, 2021). Overall, these different studies point to a strong effect of plant composition on AMF assemblages, likely resulting from both niche availability and quality.

Plant configurational heterogeneity of the microlandscape

Landscape configuration includes all characteristics that reflect spatial arrangements (Table 1; Fig. 2c). There is a wide range of theories and ample evidence for macroorganisms that report the effect of the configuration of landscape heterogeneity (Table 2) on biodiversity. Configuration can be characterized notably through the mean degree of isolation among patches of same type (at the habitat type level), the mean patch size or the type of patch interfaces (at the landscape-mosaic level) (Table 2; Fig. 2c; see Fahrig *et al.*, 2011 for a review) that likely affect species living in habitat patches. More precisely, greater isolation may decrease species fluxes among habitat patches hence selecting for those with high dispersal ability. Smaller patch size implies lower patch carrying capacity for a large number of species, whereas it increases the intensity of edge effect (Tscharnke *et al.*, 2012). The edge effect occurs at the interface of two different habitat patches and leads to changes in species composition by modifying environmental conditions, dispersal fluxes and species interactions (Ries *et al.*, 2004). Transposed to plant microlandscapes, plant configuration is defined by spatial aggregation and isolation of the different plant species within the communities (Fig. 2a,c; Table 1), and edge effect between two patches of different plants species. Such edge effect includes transfer of AMF from plant to plant, and small-scale environmental changes due to plant growth.

While most studies have focused on the effect of compositional heterogeneity on AMF, the effect of plant configuration has been largely overlooked. Existing knowledge on this topic mostly focuses on the effect of the type of interface (*edge effect*, Fig. 2c; Table 3) and of the effect of the distance to the patch interface on AMF composition (*isolation effect*, Fig. 2c; Table 1). These questions were mostly investigated in the context of plant invasions throughout the process of colonization of native communities by exotic plant species. For instance, the composition of AMF communities in rhizosphere samples near the interface between two patches of native vs exotic plants was shown to differ from the composition of those at the center of the invasive plant patch and the native plant matrix (Batten *et al.*, 2006). The effect of other components of the plant configuration (e.g. patch size, isolation) on the AMF community remains overlooked today (Table 3). To our knowledge, only one experimental study has analyzed how host–plant configuration (i.e. mean plant isolation and aggregation) influences the composition of its root AMF community: plant configuration did not influence AMF but led to significant changes in other components of plant mycobiota (e.g. Basidiomycota) (Mony *et al.*, 2020a). Further work is needed on a wider range of plant community types to investigate this relationship.

AMF dispersal at small spatial scale and floristic microlandscape connectivity

Landscape connectivity is a key concept that was developed in the 1980s; it is defined as the permeability of landscape elements to the dispersal of organisms (Table 1; Fig. 3a). Connected habitat patches are assumed to be similar in terms of species composition (Table 2). High connectivity is generally assumed to promote biodiversity by protecting local communities from the effects of isolation, while other authors point to the potentially negative effects of corridors due to the spread of competitive or pathogenic species and increased edge effects (Rosenberg *et al.*, 1997; Beier & Noss, 1998; Haddad *et al.*, 2014). Different conceptual models have been proposed including habitat corridors (i.e. a linear habitat connecting otherwise isolated habitat patches) and landscape connectivity (i.e. connectivity provided by the landscape mosaic made up of all habitat types) (Fig. 3a). While transposed to floristic landscapes, application of the connectivity concept to microbes is discussed in Mony *et al.* (2022), where emphasis is placed on the particular case of biotic connectivity provided by hosts. Biotic connectivity provided by plant distribution enables AMF dispersal through three different modes (Fig. 3b) (1) shared mycelium networks connecting different host plants; (2) AMF transfers through a host–plant connectivity structure; (3) transfer through the plant mosaic patches. A common mycelium network (CMN) built by AMF is one of the most original forms of information transfer from one host plant to the other (e.g. Giovannetti, 2008), and has no analogy among macroorganisms. Indeed, a CMN can be formed by a single fungus or when several conspecific fungal individuals connect via hyphal anastomosis and share cytoplasm (Giovannetti *et al.*, 2004; Mikkelsen *et al.*, 2008). CMN can extend from different hosts and form a single network, which can vary in

Table 3 Overview of the main hot topics to address in the future to apply the landscape ecology framework in plant–arbuscular mycorrhizal fungi (AMF) studies.

Main key prospective research questions	Key challenges	How to study them?
<i>What are the effects of plant configuration on the distribution of AMF?</i> Topic overlooked up to now because the focus has been on edge effects	Blurred boundaries between plants/ individuals that make up the landscape Importance of 3-D plant configuration because of root development along the vertical axis as well as the horizontal axis	Manipulate plant host configuration to test the effect of plant species aggregation and type of interface Analyze AMF distribution in the vertical dimension while accounting for root system architecture Develop new indices to characterize the spatial configuration of microlandscapes that integrate both the horizontal and vertical dimensions Focus on precise case studies of highly structured plant communities (e.g. clonal plant communities)
<i>What is the effect of plant connectivity on the distribution of AMF?</i> Few studies have evaluated the effect of connectivity on other groups of microorganisms (bacteria, basidiomycota, ascomycota, etc.). Transposition remains to be achieved for AMF and at small spatial scales. No studies have been conducted on actual connectivity (e.g. connectivity measured through the analysis of real movements among patches)	Need to account for response of AMF to the different host–plant species that form the landscape mosaic Dispersal distances of AMF species remain unknown	Develop functional connectivity metrics for AMF Large screening of host–plant preferences to support permeability assessment of plants to given MF species/communities Predict plant permeability to AMF dispersal through plant functional traits Determine individual AMF species dispersal at short time scales through dedicated methods (e.g. AMF labeling, microcosm experiment, etc.)
<i>What impact of the time-lag responses of AMF communities to the plant landscapes?</i> Not yet studied despite clear evidences of limitations to dispersal in AMF species	Measure the time-lag in AMF response at the appropriate time scale The timing and duration of dispersal and of root colonization by AMF species remain unknown Feedback effects of AMF distribution on plant survival, vegetative multiplication and sexual reproduction	Document the spatial distribution of plants over time in plant–AMF studies Quantify the duration and timing of the dispersal of AMF species among plants at short spatial scales Integrate the effects of AMF in the conceptual background of species coexistence (e.g. Chesson <i>et al.</i> 's models; Chesson, 1994, 2000) applied to plants

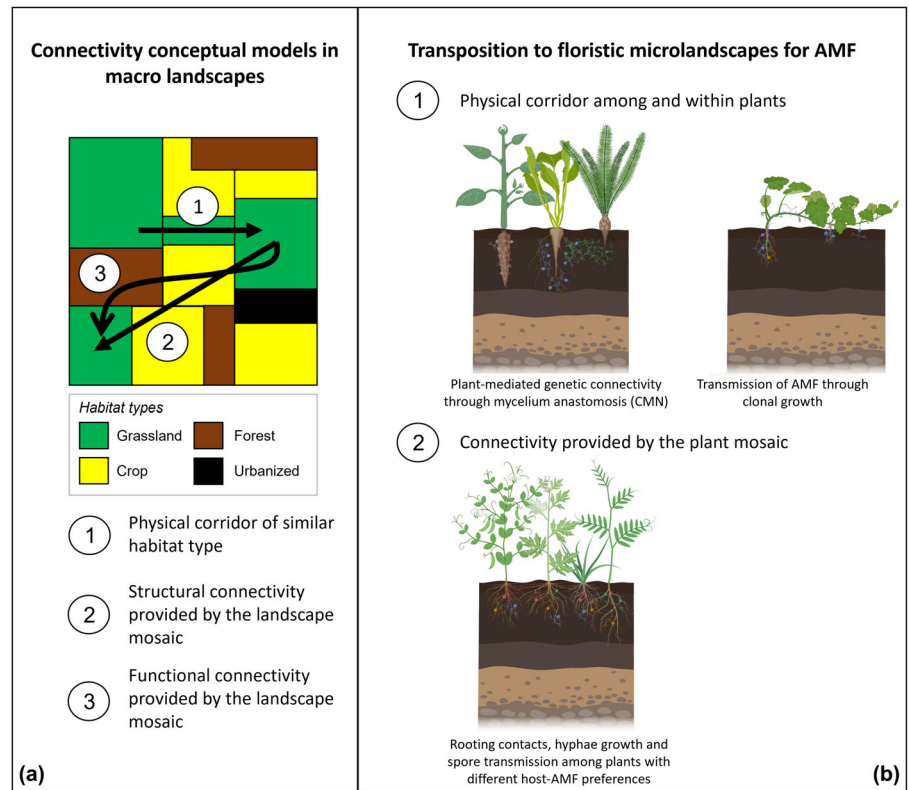
State-of the art, key challenges and suggested methods to meet these challenges are stressed.

connectedness due to the difference in hyphal structure and development among AMF (Pepe *et al.*, 2016). Through the connectivity it provides among plants, CMN can support AMF that are less cooperative for plants (Hart *et al.*, 2013) and connect mycorrhizal plants to nonmycorrhizal plants (Cosme *et al.*, 2018). To date, most research on these topics has focused on demonstrating the occurrence and role of CMN in plant performance and coexistence, but the reverse effect, that is the effect of plant distribution on the development of the CMN network development has to our knowledge, not yet been studied.

Many plants have the ability to expand spatially through vegetative multiplication and through the extension of rhizomes or stolons. The role of these horizontal stems in microbial movement has been demonstrated in pathogenic fungi (Wennstrom & Ericson, 1992), but also in the transmission of AMF and other microorganisms (Vannier *et al.*, 2016). Indeed, a subset of the mother's microbiota including AMF was reliably transmitted to daughter ramets through stolons (Vannier *et al.*, 2018), likely influencing the construction of progeny niches. Plant clonal organs may thus form a corridor that connects plant ramets belonging to the same clone. Testing landscape ecology predictions using this model would require a deeper understanding of the mechanisms behind AMF transfer, whether passive or active.

Lastly, because AMF likely disperse between hosts located a short distance apart in a step-by-step process, AMF dispersal speed and its trajectory are likely to depend on the plant mosaic. For instance, some nonmycotrophic species may form barriers to the dispersal of AMF, especially if the former are aggregated in large patches, while highly mycotrophic species may be good stepping stones (*sensu* Forman, 1995) between two given host plants. Connectivity among host plants may then be ensured by the plant mosaic heterogeneity following the concept of landscape connectivity described above. Only a few studies have tested landscape ecology predictions on AMF. In mesocosm experiments, Mony *et al.* (2020b) demonstrated that lower connectivity among host plants was related to richer and more equitable *Glomeromycota* assemblages. This result contradicts the assumption of a positive effect of connectivity on biodiversity, and suggests predominance of the edge effect, that is local neighboring plant composition that shapes AMF community composition. Interestingly, this effect was predicted more accurately when connectivity was calculated using the functional distance between plants (e.g. functional connectivity) than using Euclidean distance (e.g. structural connectivity) (Table 1; Fig. 3a). In this study, functional distances were calculated as the cumulative resistance distance between sampled host plants based on the plant mosaic seen as a binary distribution of

Fig. 3 Ecological connectivity in landscapes. (a) Conceptual models of connectivity in macrolandscapes with the example of connectivity measurement based on grassland patches (1. Physical corridor made of grasslands among grassland patches; 2. Structural connectivity provided by the grassland habitat patch distribution within the landscape mosaic (e.g. physical distance between different grassland patches); 3. Functional connectivity provided by the landscape mosaic of different habitat types among grassland patches (e.g. distance accounting permeability to dispersal of the different habitat types that make up the mosaic)). (b) Transposition of connectivity models to floristic microlandscapes for arbuscular mycorrhizal fungi (1. Physical corridor provided by CMN or transmission along clonal organs; 2. Connectivity provided by the plant mosaic). Figure created with [BioRender.com](https://www.biorender.com).



host vs nonhost plants (Fig. 2a). This result underlines the potential of transposing landscape ecology metrics for connectivity (see review by Kindlmann & Burel, 2008) to the study of AMF distribution within the plant community. Including the permeability of each host plant to AMF dispersal when assessing overall connectivity could be achieved using parameters such as plant species mycotrophy or AMF-host plant preference. The creation of large-scale databases on prevalent AMF associations for each plant species would be an asset for the development of this conceptual framework.

Temporal plant community dynamics of microlandscapes

Landscapes have been formalized as dynamic mosaics of different habitat types (*Patch Dynamic Concept*, Levin & Paine, 1974), due to local disturbances and to the turnover in some habitat types (Fig. 2c). Such temporal dynamics at patch scale throughout the mosaic have implications for biodiversity. Indeed, because the patches that make up the landscape mosaic are potentially at different stages of succession, dynamic landscapes should harbor more species than more constant landscapes (Sirami, 2016; Table 2). At the patch level the temporal dynamics of the landscape mosaic could induce delayed responses to landscape modifications due to the time required for the dispersal of organisms from one patch to another (Jackson & Sax, 2010; Lira *et al.*, 2019; Tables 1, 2). This results in community structures that are more related to the past than current landscape characteristics. When transposed to

floristic landscapes, plant communities are considered as fluctuating environments due to the spatial and temporal turnover of species (Law *et al.*, 1997), with major changes occurring at short time scales (Turkington & Harper, 1979; Thorhallsdottir, 1990; Herben & Hara, 2003), as a result of local disturbances, plant-plant interactions, differential life spans, intra-annual and inter-annual phenological changes among plants. Plant rooting systems may thus be considered as ephemeral habitat patches for AMF. These predictions – increased biodiversity in dynamic plant communities and delayed colonization of a given plant (i.e. *colonization credit*) or AMF extinction with the plant mycobiota (i.e. *extinction debt*), due to temporal changes in the surrounding plant communities – have not yet been formalized or tested. However, there is evidence for footprints left by past spatial structure of plant communities (i.e. *soil legacy*) on the soil pool of AMF available for developing plants (Bittebiere *et al.*, 2020). For example, in a mesocosm experiment in which plant composition was manipulated, the AMF assemblages of *B. pinnatum* roots were more closely linked to plant composition in the preceding year than to that in the current year (Mony *et al.*, 2020a). In another experiment, Hausmann & Hawkes (2010) demonstrated that the order in which plants established (i.e. temporal variability in the plant community) strongly affected AMF community composition in three out of the four focal plant species studied. At the short temporal scale of a few weeks, the first established plant was found to filter the available AMF pool while AMF communities converged among the second set of plants due to the presence of generalist species. This delayed response was,

therefore, better explained by the priority effect of past AMF composition and AMF–AMF interactions than by dispersal mechanisms. It would be interesting to consider larger time scales. Because in return, AMF assemblages influence the plant spatial patterns by modifying the relative abundance of plant species (Van der Heijden *et al.*, 1998) and their growth traits (Streitwolf-Engel *et al.*, 1997), it is likely that AMF influence their own future floristic landscapes, offering an original case study of dynamic landscapes, but rendering the complex ecological processes at work even harder to understand.

The floristic microlandscapes of AMF

AMF are heterogeneously distributed in plant communities and the reasons behind co-variations in plant–AMF communities have been debated and investigated for years (Kokkoris *et al.*, 2020). Most attention has focused on the driver hypothesis, demonstrating the effect of AMF on plant growth and plant–plant interactions. While a lot of experiments also investigated the host-preference effect, it would be useful to extend the concept to spatial structures in order to test the passenger hypothesis, which suggests a feedback effect of the plant community as a whole on AMF distribution. Herein, we argue that plant communities can be considered as diverse sets of AMF microhabitats arranged in space. Plant communities can thus be considered as landscapes for AMF, because AMF assemblages not only result from the additive effect of patchy environmental conditions but also from patch interrelations. However, while the effect of plant compositional heterogeneity has been tested in many studies, the effect of configurational heterogeneity, of plant patch connectivity, and of plant dynamics on AMF assemblages has been poorly tested (Table 3). The wide theoretical background with the precise predictions presented above, mostly based on landscape ecology theories, could be applied to fungal assemblages to improve our understanding of their distribution at small spatial scales.

More specifically, this article pinpoints several prospects at the cutting edge of research (Table 3): Investigating the effect of plant configuration on AMF assemblages, both at the landscape-mosaic level (configuration heterogeneity) and at the habitat type level (i.e. connectivity among given host plants). These questions require precise manipulation of plant spatial distribution following the same protocols as those used in landscape manipulation (Jenerette & Shen, 2012). Improving predictions of the effect of plant distribution on AMF assemblages could be achieved by better understanding AMF-preferential associations and define predictors based on plant functional traits and related with AMF niche quality (e.g. root biomass per root diameter size), AMF small-scale dispersal among plants (e.g. root morphology), plant spatial expansion and temporal turnover (e.g. root lifespan, clonal growth, and traits related to competition with other plants). Manipulation of the functional composition of plant communities at the individual plant-trait resolution is a promising way to investigate this question. A precise understanding of AMF dispersal within the floristic environment is essential for future research aimed at developing a landscape ecology framework adapted to fine-scale AMF assemblages.

Beyond AMF, the plant microbiota comprises a tremendous diversity of microorganisms with varying lifestyles and significant consequences for plant establishment and survival. While herein we focus on AMF because of their biotrophic lifestyle that link their distribution to that of the plants, the concept may apply to and benefit the understanding of other plant-associated microbes. For example, bacterial species do display different host preference and invasiveness toward plant species even if they are not tightly linked to plant communities (e.g. Wipfel *et al.*, 2021). Whether this type of process determines microbial dispersal in plant communities and contributes to the overall microbial distribution patterns remains to be tested experimentally, which requires a framework that considers microbial fluxes at small scale. Moreover, because other microbes like bacteria also interact with AMF in mutualistic (mycorrhiza helper bacteria, Frey-Klett *et al.*, 2007) or antagonistic ways (e.g. Miransari, 2011 for a review), they also likely contribute to the observed AMF distribution.

Overall, beyond a better understanding of small-scale AMF distribution, exploring the drivers that shape AM fungal communities is essential to predict and possibly manipulate their composition and to influence the associated ecological functioning (Table 2). As recently exemplified by Lutz *et al.* (2023) in large-scale field inoculation trials with AMF, sustainable agriculture may rely on the functions AMF provides to plants (e.g. nutrient acquisition, stress tolerance, disease resistance). Although multispecies mixtures of plants have been suggested as an alternative to conventional cropping system, little attention has been paid to how these species should be arranged spatially (i.e. spatial configuration) to better promote the spread of AMF across plants, and how changes in the mixtures over time would affect the local reservoir of symbiotic AMF. The landscape ecology framework provided herein, that has demonstrated strong influence of configuration both at the landscape mosaic and the patch level on biodiversity, and applied at a microscale here should help support innovations in crop management, and more generally in plant production.

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Competing interests

None declared.

Author contributions

CM, NV, FB, AE and PV contributed to discussion about applying landscape ecology concepts to AMF. CM wrote the manuscript, and the other authors reviewed and approved the final draft.

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