

Chapter 13

Soil Biota as Drivers of Plant Community Assembly



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13.1 Introduction

Soil organisms affect ecosystem processes, such as carbon (C) and nutrient cycling (Nielsen et al. 2011; De Graaff et al. 2015), plant productivity (van der Heijden et al. 1998; Wagg et al. 2011), and the response of ecosystems to climate change and increased atmospheric nitrogen (N) deposition (de Vries and Shade 2013), through their influences on plants (Wardle et al. 2004). The effects of soil biota on plant growth, performance, and productivity are relatively well studied (e.g., Bradford et al. 2002; Kulmatiski et al. 2014), but less is known about how soil biota drive plant community assembly (Bennett and Cahill 2016; Sikes et al. 2016), namely, how local assemblages are constructed from the regional species pool. This knowledge is crucial in predicting long-term and large-scale ecosystem processes and how plant communities reassemble in response to environmental changes (Kardol et al. 2013).

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Soil biota can affect plants both directly and indirectly (Wardle et al. 2004). Direct effects can result from the accumulation of pathogens and root herbivores (e.g., van der Putten et al. 1993) and from associations with mutualistic soil organisms such as mycorrhizal fungi or N-fixing bacteria (e.g., Teste et al. 2017). Indirect effects can result from the impacts of soil organisms on soil properties and nutrient dynamics (e.g., Zhang et al. 2016). In this chapter, we discuss how these direct and indirect effects of soil biota modify how plant communities assemble, from local-scale priority effects to broad-scale vegetation dynamics. We discuss soil biota-mediated *niche modification* and *soil legacy effects* and how these forces can drive plant community assembly by affecting (1) plant-competitive and facilitative interactions, (2) species replacements, and (3) patterns of coexistence and community diversity. Finally, we discuss primary and secondary succession, biodiversity conservation, plant invasion, and how current and projected global environmental changes may alter the impacts of soil biota on plant community assembly.

13.2 Niche Modification, Priority Effects, and Soil Legacies

Soil organisms can sway the selection of species able to coexist in the community through niche modification, such as changes in soil properties and microclimate and associations with plant roots that favor or suppress certain species in the plant community. Figure 13.1 depicts how different functional groups of soil organisms and soil biodiversity affect plant community composition through the selective assembly of species.

Soil bioturbators, such as earthworms and termites, can affect soil properties directly by altering the physical structure of the soil environment, such as soil porosity (Lavelle et al. 1997). These physical alterations influence the movement of water through the soil profile and often result in increased soil N availability (van Groenigen et al. 2014). As such, bioturbators can stimulate plant growth, but their effects are species-specific, favoring resource-acquisitive species that are the strongest competitors for N (Wurst et al. 2005) (Fig. 13.1a). Furthermore, saprotrophic soil organisms change soil nutrient availability by decomposing and mineralizing dead plant-, animal-, and microbe-derived organic matter, making nutrients available again for plant uptake (Wardle et al. 2004). In general, saprotrophs stimulate plant growth, allowing more individuals to coexist (Fig. 13.1b). However, an increase in the ratio between fungal and bacterial energy channels in the decomposer food web is typically associated with reduced nutrient cycling and low rates of nutrient supply to plants (Wardle et al. 2004), reducing the total number of individual plants and increasing the competitive ability of slow-growing, resource-conservative species over fast-growing, nutrient-acquisitive species within the plant community (Fig. 13.1c).

Plant species vary in their susceptibility to root pathogens and herbivores (Brown and Gange 1990). Fast-growing species are often more susceptible than slow-growing species because of trade-offs between investment in growth and

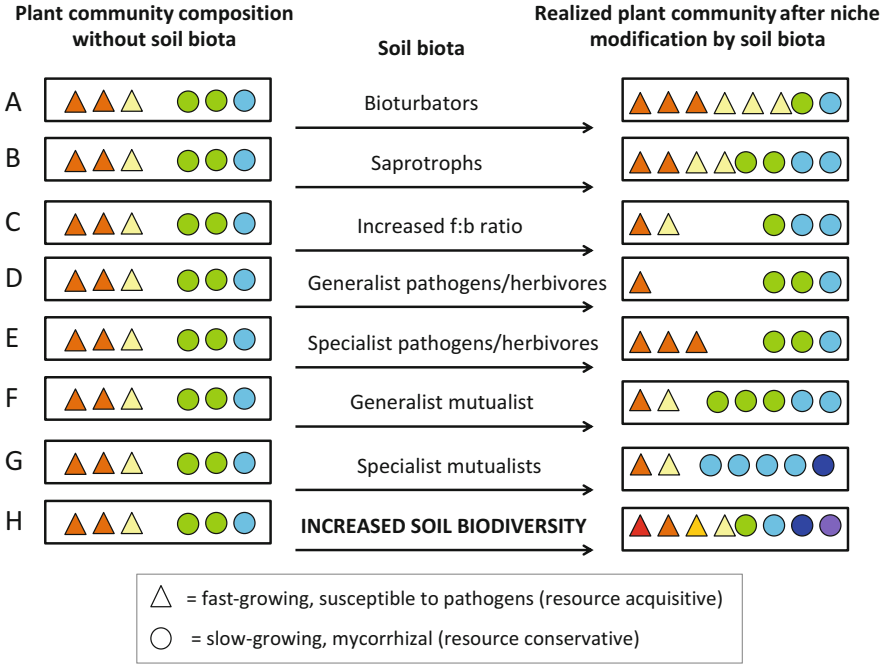


Fig. 13.1 Hypotheses on how soil organisms may modify niches and affect plant community assembly through niche modification. Shown are hypothetical plant communities where each symbol represents one individual plant. Triangles represent fast-growing, resource-acquisitive species which are susceptible to root herbivores and pathogens. Circles represent slow-growing, resource-conservative species which are less susceptible to root pathogens but may more strongly depend on root mutualists such as mycorrhizal fungi. Different colors denote different species. Soil biota can shift community density or productivity as indicated by the number of individuals present in the realized community and by shifting species composition. (a) Bioturbation increases soil N availability, which promotes fast-growing plant species at the expense of slow-growing species. (b) By decomposing litter and soil organic matter, saprotrophic organisms increase nutrient availability (i.e., increased niche size), which allow more individuals to coexist. (c) An increase in the soil fungal to bacteria ratio slows down nutrient cycling, which both constrains the number species able to coexist and reduces the performance of nutrient-demanding resource-acquisitive plant species. (d–e) Pathogens tend to reduce the abundance of fast-growing species while mutualists (f–g) often promote the abundance of slow-growing species. (h) Overall, the increase in soil biota diversity favors species coexistence and plant community diversity

reproduction versus investment in defense mechanisms and longevity, respectively (Reynolds et al. 2003). Hence, generalist pathogens and herbivores would reduce available niche space with stronger consequences for fast-growing than for slow-growing species (Fig. 13.1d). Specialist root pathogens and herbivores, such as certain plant-feeding nematodes, may cause local species extinction, which would release the remaining species from competition (Fig. 13.1e). Generalist mutualists enhance plant community resource utilization, thereby increasing the number of individuals and species able to coexist and favoring those species associating with the mutualists (Fig. 13.1f). In contrast, specialist mutualists selectively benefit their

host species, gaining them competitive advantage over other species (van der Heijden et al. 1998; Hoeksema 2005), which could reduce community diversity (Fig. 13.1g). However, specialist mutualists could also facilitate the establishment and persistence of species that would otherwise be absent. Finally, increased soil biodiversity may increase niche space, which could stimulate plant community productivity and species coexistence (van der Heijden et al. 1998; Wagg et al. 2014) (Fig. 13.1h).

Variation in the composition and diversity of soil biota can result from geographical segregation and environmental constraints (Classen et al. 2015). Together these forces determine the regional soil species pool. Variation in the composition and diversity of soil biota can also result from local feedbacks with plants (Bardgett and van der Putten 2014). Plants exert species-specific effects on the soil community through the input of species-specific litter (both root- and shoot-derived) to the soil and through the accumulation of pathogens, herbivores, and mutualists in their rhizospheres (van der Putten et al. 2013). Such species-specific effects not only influence competitive interactions and dominance patterns, but can also result in persistent biotic soil legacies, thereby driving temporal species replacements and possibly longer-term community dynamics (Kardol et al. 2007) (Fig. 13.2). As such, soil biota may cause priority effects, where plant-competitive interactions and community dynamics depend on the timing and order of species arrival (Chase 2003; Fukami 2015). Early-arriving species can preempt and modify available niches for later-arriving species through their effects on soil biota, causing long-lasting historical contingency effects (Kardol et al. 2007; van de Voorde et al. 2011) (Fig. 13.2). For example, plant species-specific effects on the soil microbial community may carry over to affect the relative abundance of plant species at a later stage (Kardol et al. 2007). Along the same lines, mycorrhizal fungi can modify the priority effects of early-arriving species on plant community diversity and community composition (Burkle and Belote 2015). Moreover, root and shoot herbivores may directly and indirectly affect soil microbial communities, which in turn can create soil legacies for the next generation of plants (Kostenko et al. 2012; Sonnemann et al. 2013).

Can we scale species-specific effects up to the ecosystem level? It is not well understood how the above-described priority and historical contingency effects resulting from plant interactions with soil biota persist in longer-term plant community dynamics and whether historical contingency effects would be amplified over time (Fukami and Nakajima 2013; Fukami 2015). However, feedbacks with soil biota have been shown to explain relative species abundance in tropical forests (Mangan et al. 2010) and grasslands (Klironomos 2002) and maintain the high diversity in Mediterranean-climate shrublands (Teste et al. 2017) (Fig. 13.3). These feedback effects are often explained by soil-borne pathogens promoting local plant species coexistence and diversity via conspecific negative density dependence (Bever et al. 2015). Studies have shown how local soil pathogen abundance can explain the distribution of neighboring plant species (Gómez-Aparicio et al. 2012) and the assembly of plant communities across large spatial scales (Blomqvist et al. 2000). Other studies have shown that soil biota can affect plant communities

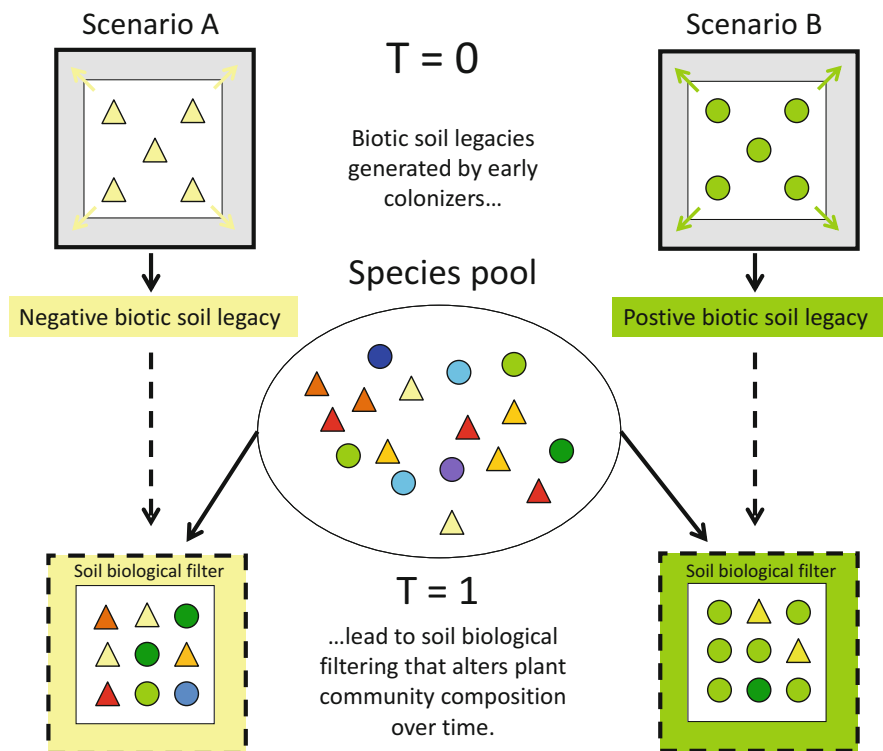


Fig. 13.2 Hypotheses on how soil biota may affect temporal plant community assembly through plant–soil feedback and the provisioning of biotic soil legacies. Shown are hypothetical plant communities where each symbol represents one individual plant. Triangles represent fast-growing, resource-acquisitive species which are susceptible to root herbivores and pathogens. Circles represent slow-growing, resource-conservative species which are less susceptible to root pathogens, but may more strongly depend on root mutualists such as mycorrhizal fungi. Scenario A indicates negative plant–soil feedback for the early-arriving species ($t = 0$), creating more available niche space for the establishment of other, heterospecific individuals at the later successional stage ($t = 1$). Scenario B, on the other hand, indicates positive plant–soil feedback for the early-arriving species ($t = 0$), creating more available niche space for conspecific individuals to establish at the later successional stage and, hence, less available niche space for heterospecific individuals ($t = 1$). Further, the species-specific effects of the early-arriving species on the soil biological communities determine which heterospecific species are able to establish at the later successional stage

through altering plant-facilitative interactions (Montesinos-Navarro et al. 2016). For example, common mycorrhizal networks can connect multiple plant species and promote the establishment of other plants near the original host plant (Moora and Zobel 2009). The effects of soil pathogens and mycorrhizal networks on neighboring plant species vary among plant species (van der Heijden and Horton 2009). In other words, the resident plant community creates a soil biological filter, which could drive larger-scale plant community dynamics.

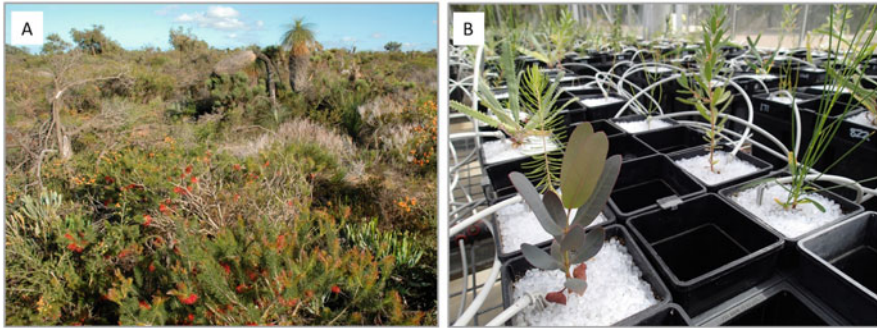


Fig. 13.3 Feedback with soil biota maintains high plant diversity of Mediterranean-climate shrublands, as shown by Teste et al. (2017). In a glasshouse experiment, 16 co-occurring plant species with different nutrient-acquisition strategies were grown in the presence of soil biota from under their own or other plant species. Feedbacks with soil biota varied with nutrient-acquisition strategy, and computer simulations showed that these feedbacks were strong enough to promote species coexistence and maintain high plant community diversity. (a) Example of a hyperdiverse shrubland near Lesueur National Park, Western Australia (photo credit and copyright © Etienne Laliberté). (b) Impression of the glasshouse experiment testing plant responses to soil biota (photo credit and copyright © François P. Teste)

13.3 Primary and Secondary Succession

13.3.1 Primary Succession

Vascular plants are generally slow to establish during primary succession (Fig. 13.1) on newly exposed surfaces such as glacial moraine, cooled volcanic lava, mobile sand dunes, or mine tailings (e.g., Bardgett et al. 2007). Slow establishment cannot be explained solely by dispersal limitation. Harsh conditions and low soil N availability are among the primary constraints (Vitousek et al. 1993; Laliberté et al. 2012; Titus and del Moral 1998). Soil organisms can facilitate the initial stage of plant community assembly through niche modification. In primary succession, plant community assembly is generally preceded by a heterotrophic phase, i.e., aerial deposition of highly dispersive invertebrates and/or allochthonous detritus that provides the initial inputs of energy and nutrients (e.g., Hodkinson et al. 2002; Bardgett et al. 2007). Soil organisms, including microbes, testate amoebae, large invertebrates, are often windborne and may establish on newly exposed surfaces well before vascular plants (Hodkinson et al. 2002; Wanner et al. 2015), facilitated by allochthonous inputs of organic matter (Brankatschk et al. 2011).

Initial soil communities may conserve nutrients (particularly N) and as such facilitate the establishment of vascular plants. Further, the defecation and death of early-arriving soil animals initiates decomposition and thus gradual soil formation, further steering the trajectory of plant community assembly. For example, Bardgett et al. (2007) found that early-colonizing microbes were initially supported by “old” C and that only after more than 50 years of organic matter accumulation was the soil

microbial community primarily supported by plant-derived C. Community assembly of saprotrophic microbes (Kazemi et al. 2016) and testate amoebae (Wanner et al. 2015) can be highly variable initially and converge later, likely as a response to plant colonization. Inputs of nutrients and organic matter during early ecosystem development are generally dominated by microbial C and N fixation (Schmidt et al. 2008). In addition, the biomass of the soil meso- and macrofauna can increase rapidly (Kaufmann 2001; Bokhorst et al. 2017) long before plant arrival and may further contribute to niche modification and diversification during primary succession.

In primary succession, soil nutrient concentrations are often low. Therefore, early-arriving plant species may depend on associations with soil organisms for capturing nutrients. For example, the earliest colonizing plants on infertile volcanic substrates are often legumes, in part because of their ability to fix atmospheric N₂ via symbiosis with rhizobia bacteria (Wang et al. 2012). The N fixed by these legumes is ultimately incorporated in the terrestrial N cycle. Since many legume species have poor long-distance dispersal mechanisms, (re-)colonization of volcanic substrates may proceed slowly (del Moral 1983). Once legumes have established, they may facilitate the establishment of other species through increased niche availability (Vitousek et al. 1987). During later stages of succession, rhizobia may further shape community assembly by influencing soil N cycling and, hence, plant resource competition. For example, it is known from mesocosms simulating early-successional plant communities that rhizobia specializing on the dominant plants can shift competitive interactions and community composition. Thereby, such specializations can negatively impact on community diversity through a combination of both inhibitory and facilitative effects (Keller 2014). Additionally, mycorrhizal fungi can also affect plant community assembly after volcanic eruptions. Initial plant colonization after volcanic eruption often includes plants without obligate dependency on mycorrhizal partnerships, but facultative species also colonize soon after (Obase et al. 2008). Mycorrhizal spores may be brought in by wind dispersal, and previous studies showed that facultative mycorrhizal species arrive and establish relatively early during primary succession (Allen et al. 1992; Nara 2006). Once established, short-distance dispersal occurs and the mycorrhizal network may expand, facilitating the establishment of other plant species that depend on mycorrhizae.

In foredune succession, soil-borne diseases and root herbivores modify plant-competitive interactions, feedbacks, and species replacements, driving initial plant community assembly (e.g., van der Putten et al. 1993; Brinkman et al. 2005). For example, in the Dutch foredunes, the first-arriving plant species, *Ammophila arenaria*, suffers from species-specific soil-borne diseases, giving room for succeeding species that are more tolerant of or immune to the soil-borne diseases of their predecessors (van der Putten et al. 1993). Root-feeding nematodes also affect plant community dynamics (Brinkman et al. 2015). For example, van der Stoep et al. (2002) used bioassays to demonstrate that the endoparasitic nematodes *Heterodera arenaria* and *Pratylenchus* spp. rapidly built up in the root zone of *A. arenaria* and coincided with a negative soil feedback. However, subsequent work by Brinkman et al. (2005) indicated that negative feedback generated by *A. arenaria* could not

solely be explained by root-feeding nematodes and most likely were caused by more complex interactions among different groups of soil organisms.

13.3.2 Secondary Succession, Ecosystem Restoration, and Biodiversity Conservation

While primary succession starts from newly exposed surfaces, virtually lacking any soil life, secondary succession is the process of species colonization and replacement which begins with some biological legacy following an initial disturbance or the cessation of agricultural or forest management. The soil biotic legacy (Fig. 13.2) depends on the pre-disturbance condition or the former land use. For example, after abandonment of agricultural land, densities of soil pathogens and root herbivores may initially be high, and the saprotrophic microbial community is often dominated by bacteria rather than by fungi (i.e., a low F:B ratio, see Fig. 13.1). This is mostly because agricultural management negatively affects saprotrophic and mycorrhizal fungi (van der Wal et al. 2006) (see also Sect. 5.2). Similarly, other natural or human-induced disturbances such as mining, wildfire, wind throws, and clear-cuts affect soil communities. These disturbances affect some taxa or functional groups more than others, confronting early-arriving plant species with a distinct soil biotic legacy (e.g., Banning et al. 2011). For example, after coalmine reclamation, degraded mycorrhizal communities could delay or inhibit the establishment of later-successional species (Bauman et al. 2013).

After initial plant establishment, soil biota can further control succession through the influence of early-successional species on the soil community. In secondary succession on ex-arable land in the Netherlands, early-successional species create negative soil feedbacks through species-specific buildup of soil microbial pathogens. These feedbacks reduced the competitive strength of early-successional species and thus accelerated succession (Kardol et al. 2006). In addition, early-arriving species can have selective soil legacy effects on the growth of other plant species (Kardol et al. 2007; van de Voorde et al. 2011). Moreover, the legacy effects of early-successional grasses on mid-successional grasses through soil microbial community development were more pronounced than effects on forbs (Kardol et al. 2007). As such, soil biotic legacies can drive the direction in which a plant community develops. It is unclear how long plant species-specific soil legacies last (Wurst and Ohgushi 2015), but plant community dynamics at any stage of ecosystem development may in part reflect soil community influences from the past.

Soil biota affect the rate and direction of community assembly during secondary succession, but can also drive community diversity. In a greenhouse experiment, De Deyn et al. (2003) showed how invertebrate soil fauna from a series of secondary sward successional stages selectively suppressed fast-growing, early-successional dominant plant species, and thereby enhanced the relative abundances of subordinate species and species from later succession stages. These effects were most likely due

to root-feeding nematodes and Elateridae larvae selectively feeding on the roots of otherwise dominant grasses. A follow-up experiment further suggested that root-feeding nematodes reduced the effects of nutrient supply on plant dominance, leading to an increase in plant community diversity (De Deyn et al. 2004). Additionally, plant diversity can also be enhanced through subordinate plants benefitting from associations with mycorrhizal fungi (Gange et al. 1990; de Leon et al. 2016). Kardol et al. (2006) showed that late successional plant species displayed positive feedbacks, particularly with soil organisms, most likely mycorrhizal fungi, from later successional stages. This suggests that the absence of appropriately compatible mycorrhizal spores after disturbances, such as an intensive agricultural land-use (see Sect. 13.5.2), could delay plant community succession.

Can the rate and direction of changes in plant community assembly be manipulated? Evidence for the importance of soil biota in successional plant communities (Kardol et al. 2007) and the notion that plant community development may be constrained by slow dispersal of soil mutualists (e.g., mycorrhizae) (Eschen et al. 2009; Zobel and Opik 2014) suggests that manipulation of soil biota could be used in restoration of degraded plant communities. Ecosystem restoration after human disturbances represents a special case of secondary succession where the initial assembly order of plant communities may determine whether or not communities develop towards the desired “target state.” Here, plant community assembly can be assisted by artificially modifying species arrival order by sowing or planting species that would not naturally colonize the restoration site (Kardol et al. 2009; Burkle and Belote 2015). However, establishment of the desired species can depend on the absence or presence of soil biota (Hodkinson et al. 2002). Simultaneous introduction of plant propagules and soil organisms from a target site may enhance plant community succession (Middleton and Bever 2012) and, moreover, may be more effective than introduction of plant propagules or soil organisms alone.

Attempts to use soil inoculation to enhance ecosystem restoration have not always been successful (Hedlund and Gormsen 2002; Aprahamian et al. 2016), often because of a lack of compatibility in abiotic soil conditions between the “donor” and the “receptor” sites (Kardol et al. 2009). Some studies, however, have shown how soil inoculations can be used to assist the restoration of plant assemblages. In a greenhouse study, Carbajo et al. (2011) found, for example, that inoculation of soil from late-successional grassland into ex-arable land promoted the competitive ability of target plant species. Furthermore, there is evidence that these beneficial effects of late-successional soil may result from enhanced mycorrhizal associations. Indeed, in tallgrass prairies, Koziol and Bever (2015, 2016) found that late-successional plant species were more responsive to mycorrhizal inoculation than early-successional species and had a higher degree of specificity to different mycorrhizal species. In line with these findings, Helm and Carling (1993) demonstrated that soil transfer from intermediate and late-successional stages was effective in establishing plant-mycorrhizal associations in reforestation on abandoned mine lands. Similar results were found for the establishment of late-successional target species on ex-arable land (Eschen et al. 2009) and for seedling establishment in degraded drylands (Pineiro et al. 2013).

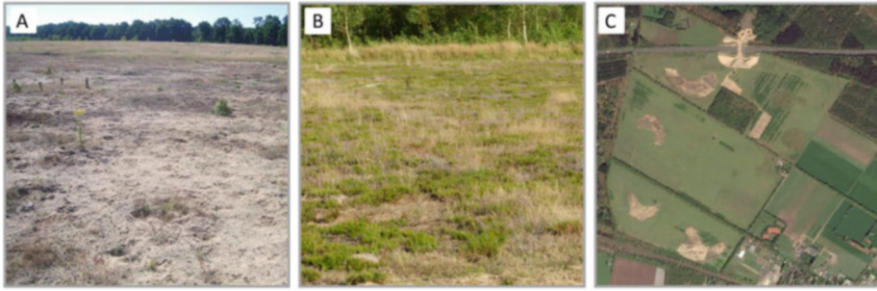


Fig. 13.4 Effects of inoculation with heathland soil on plant community assembly during secondary succession on ex-arable land in the Netherlands after top soil removal (Wubs et al. 2016). (a) Control plot without soil inoculation, and (b) Plot inoculated with heathland soil (photo credits and copyright © Jasper Wubs). (c) Aerial view of the experimental area: in the lighter areas, the top soil is removed. Within these areas, some darker parts are inoculated with heathland soil (Google Earth). All photos were taken approximately 7 years after set up of the experiment

However, detailed knowledge on which soil communities would promote a certain successional trajectory (Perring et al. 2015) is still lacking. Probably the best example so far of the manipulation of soil biota to control plant community development comes from a recent study by Wubs et al. (2016) (Fig. 13.4). They established a large-scale experiment on ex-arable land and tested for the effects of soil inocula from different origins (i.e., a grassland restored more than two decades ago or a dry heathland) on plant community development. Different origins of the soil inocula steered plant communities into the directions one would anticipate (i.e., towards grassland or heathland vegetation, respectively, depending on inocula origin) (Fig. 13.4).

Finally, what is the role of soil biota in the conservation of diverse plant communities? In Australian shrubland, Teste et al. (2017) found that plants of contrasting nutrient strategies [i.e., N-fixers, arbuscular mycorrhizal (AM), ectomycorrhizal (EM)] experienced different plant–soil feedbacks. These feedbacks were strong enough to at least partly explain the high levels of plant diversity observed in this system (Fig. 13.3). Additionally, Rodriguez-Echeverria et al. (2013) found that specific bacterial communities were associated with benefactor and beneficiary plants and that the positive effects of the soil biota on the beneficiary plants were independent of the benefactor. This shows that the legacy effect of a specific plant on soil biota can have far-reaching consequences. Essentially, specific groups of soil organisms can shape facilitation relationships between plants and might, therefore, promote community diversity. Furthermore, soil biota can play a role in modifying competitive interactions between plants in a way that can enhance diversity. For example, Pendergast et al. (2013) showed that in North American old fields, soil communities from contrasting origins determined whether or not intraspecific interspecific competition was stronger, all the while maintaining the dominance of the forb *Solidago canadensis*. This indicates that the diversity of subordinate species within a plant community may be maintained by complex biotic

plant–soil feedback and competitive interactions. In line with this, Maron et al. (2016) used alpine grassland species to show that biotic plant–soil feedbacks were the likely cause of maintained diversity, while competition between species was less important in heterospecific soils versus conspecific soils. This could mean that in this alpine system, the soil community is a stronger player in maintaining plant community diversity than competition. In summary, there is a need to consider complex plant–soil biota interactions when developing programs to preserve plant biodiversity.

13.4 Plant Invasions and Native Range Expansions

13.4.1 *Invasive Plants and Priority Effects via Soil Biota*

Invasive plants cause ecological and economic damage (van Kleunen et al. 2015) and pose one of the largest threats to global biodiversity (McGeoch et al. 2010). One way that invasive plants might interact with the soil community to affect their own future dominance in a system is through soil-mediated priority effects (Fig. 13.2). Priority effects may involve competition between plants for resources (Grman and Suding 2010) or accumulation of allelochemicals in the soil (Bais et al. 2003). However, the advantage of enhanced competitive ability amongst invasive plants tends to diminish with increasing time since invasion (Gioria and Osborne 2014). For example, Lankau et al. (2009) found that in North America, the invader *Alliaria petiolata* produced chemicals that the local soil community is initially incapable of breaking down. However, with increasing time since invasion, the soil decomposer community adapted to cope with the chemical compounds produced by *A. petiolata*. This finding indicates that over time, the soil community might mitigate the allelopathic effects of an invader, allowing for the resurgence of native plants, subsequent compositional changes to the plant community, and further niche modification.

Soil legacy effects (Fig. 13.2) may in part explain why invasive plant dominance might persist. Such soil legacies can manifest in different ways. For example, Kuebbing et al. (2016) found that the nonnative woody shrubs *Lonicera maackii* and *Ligustrum sinense* generated significant (likely biotic) soil legacies. This led to decreased native plant community root biomass, possibly resulting in reduced presence of native plants in the community over time. In further support of this, Eppinga et al. (2006) found that the invasive grass *Ammophila arenaria* promoted the accumulation of native pathogens, which subsequently excluded native plant species. Moreover, Stinson et al. (2006) found that *A. petiolata* produced chemicals that disrupted the mutualistic relationship between tree seedlings and mycorrhizal fungi, essentially changing the types of plants that could establish. Exclusion of native tree seedlings due to changes in the soil mycorrhizal community could potentially alter the overstory plant community composition or even pave the way for the establishment of additional invaders, generating an “invasional meltdown” (Simberloff and Von Holle 1999; Simberloff 2006; O’Dowd et al. 2003; Green et al. 2011), although

evidence for such invasional meltdowns involving plants and the soil community is rare (but see Paudel et al. 2016).

Alternatively, the relaxation of the soil biotic filter may contribute to plant invasion. The enemy release hypothesis suggests that invasive plants proliferate in new ranges because they have escaped above- and belowground pathogens from their home ranges (Maron and Vila 2001; Keane and Crawley 2002). For example, Gundale et al. (2014) found that the North American native *Pinus contorta* performed better when grown in soils from its nonnative range in Sweden than when grown in soils from its home range. These differences in growth were the result of the soil biotic community. Although *P. contorta* has yet to become invasive in Sweden, it is invasive in other nonnative ranges, such as New Zealand and Argentina (Dickie et al. 2014; Bravo-Monasterio et al. 2016). Therefore, there is concern that its highly competitive growth could eventually allow it to outcompete native species in Sweden, such as *Pinus sylvestris* and *Picea abies* (Despain 2001). This could result in an altered tree species community composition due to a cascade effect initiated by the soil biotic community, particularly if *P. contorta* invades areas above the tree line or grasslands that are naturally devoid of trees (Bravo-Monasterio et al. 2016). Essentially, invasion by *P. contorta* leads to the occupation of an unfulfilled niche, resultantly modifying the realized niche of other plant species (i.e., grasses, forbs) that used to dominate the plant community.

Maron et al.'s (2014) study supports the enemy release hypothesis at a regional scale. Six perennial European forb species exhibited no negative plant–soil feedbacks in their introduced North American range, while negative feedbacks tended to occur when they were grown in European soils. Soils were collected from across a wide regional scale, suggesting that these effects were generated by soil biota with a large spatial distribution. In another study, Diez et al. (2010) found in their survey of New Zealand invasive plants that with increasing time since invasion, the soil biotic community generated greater negative feedbacks. Although this study showed higher invasive plant abundance to be associated with increasingly negative soil feedbacks, such negative feedbacks may lead to suppression of the invaders.

Changes to the soil biotic filter wrought by invasive plants might not always be proportional or consistent; namely, benefits or detriments of the soil biotic filter might affect both native and invasive species, but the effects might not be equivalent within a group. In old fields in Tennessee, USA, Stuble and Souza (2016) found that the effects of early arrival were beneficial to both native and exotic plants, but the effects of later arrival were disproportionately negative for natives compared to exotics. Further, Sikes et al. (2016) found that the growth rates of the exotic grass *Melinis repens* and the native grass *Schizacharyium niveum* were negatively affected when each species was grown in soils with its “home” fungi. However, this negative priority effect was negated when other plants or fungi from different sites were introduced earlier, illustrating how the assembly of plant and soil communities interact. Conversely, Molina-Montenegro et al. (2015) showed that the Chilean alpine cushion plant *Laretia acaulis* promoted fungal endophytes that facilitated the survival of both native and exotic plant seedlings. These findings indicate that both negative and positive conditioning of soil biotic communities can occur. Even if

initial facilitative relationships do not occur, over time invasive plant species might develop mutualistic relationships with belowground organisms such as mycorrhizae (Callaway et al. 2004) or decomposers (Liao et al. 2008). These examples demonstrate that invasive plants interact with the soil biota in ways that could change biotic filters, leading to their persistence (i.e., via filtering that favors invasive plants due to enhanced mutualisms) (Callaway et al. 2004) or decline (i.e., via filtering that disfavors invasive plants due to rapid evolution of soil pathogens) (Bardgett and van der Putten 2014).

What role do biotic communities play during restoration efforts that aim to eradicate invasive plants? Simply removing invasive plant species from an ecosystem may not be enough to affect restoration. The soil legacy effect of an invasive plant can alter the soil biota, which could make it impossible for native plants to reestablish. For example, in disturbed and pasture sites in Florida, USA, that were, respectively, invaded by the grasses *Melinis repens* and *Paspalum notatum*, Hamman and Hawkes (2013) found that restoration efforts were more successful when a soil inoculum from under native plants was added. However, the effect of soil biotic inoculum was site-specific, with sites that were more heavily invaded experiencing less successful restoration. Furthermore, removing *Pinus contorta* trees from a New Zealand forest left a legacy of EM fungi, which facilitated the establishment of another invasive tree, *Pseudotsuga menziesii*, and shifted the soil community to bacteria-based channels (Dickie et al. 2014). In line with these findings, Kulmatiski et al. (2006) discovered that invasive plants tend to dominate in abandoned agricultural fields in Washington, USA, due to beneficial fungal populations and faster nutrient cycling (likely due to changes in soil biota), with competition playing a relatively minor role in determining plant community composition.

13.4.2 Range Expansion

In addition to inter-continental plant invasion, global climate change and alterations to land use (for further details, see Sect. 13.5) have caused intra-continental plant range expansion (van der Putten et al. 2010). Range expansion of specific plant species can lead to alterations to the local plant community (van der Putten 2012) and plant–soil organism interactions (van der Putten et al. 2013). Plants that expand their ranges might benefit from lower accumulation of rhizosphere pathogens, resulting in reduced negative plant–soil feedback effects (Engelkes et al. 2008), similar to what invasive plants experience in line with the enemy release hypothesis. For example, Morriën and van der Putten (2013) found that range-expanding plants tended to harbor fewer *Fusarium* spp. (a genus of pathogenic fungi) in their rhizospheres compared to native congeners. Smaller negative soil effects could in part explain range expansion. However, certain plant species might expand into a range where they find a mismatch with the local soil community, given that soil organisms are presumably relatively poor dispersers (Classen et al. 2015). A

literature survey by Berg et al. (2010) showed that most organisms across trophic groups appeared to have contrasting dispersal abilities, but little evidence has been obtained to determine if mismatches between plant and soil communities exist (van der Putten 2012).

The relationship between range-expanding plants and the soil biotic community is often not unidirectional. For example, top-down and bottom-up control of parasitic nematodes can vary at the interspecific level in range-expanding plants and their native congeners (Wilschut et al. 2016). Additionally, van Grunsven et al. (2007) found that range-expanding plants experienced less negative plant–soil feedbacks in their expanded range than in their native range. However, nutrient availability altered these effects. Therefore, broad conclusions may not be possible when predicting these interactions. Furthermore, range-expanding plants might fill a modified realized niche in their new range, leading to changes such as altered nutrient cycling or primary productivity (van der Putten 2012). Finally, although the soil community in a plant's new range can often control the success or failure of expansion, range-expanding native plants themselves can have both direct and indirect impacts on the soil microbial community. Collins et al. (2016) showed that the native sagebrush *Artemisia rothrochii* increased soil bacterial diversity both directly and indirectly via changes to soil organic N and C stocks. Changes to the microbial community as driven by a single range-expanding species could have far-reaching impacts on the assembly of the entire plant community over time that trump the effects of the original soil community. On the other hand, the loss of soil biota could result in plant range contraction, or in certain circumstances the presence of soil biota might even delay plant range contraction (Lankau et al. 2015). However, experimental evidence testing these hypotheses is rare.

13.5 Global Environmental Change

13.5.1 Climate Change

Climatic change is expected to modify the structure of plant communities. Numerous forms of climate perturbations, such as drought, warming, and elevated [CO₂] are occurring simultaneously, generating uncertainties in predicting the reassembly of plant communities. For example, increases in atmospheric CO₂ concentrations can accelerate succession by promoting the growth of late successional plant species and thus increasing their dominance in the community (Polley et al. 2003). By contrast, shifts in precipitation regimes can delay succession as disturbances, such as floods, drought, and fire often favor early successional communities and limit the arrival or the growth of late successional species (Laflower et al. 2016). Overall, the response of plant communities to climate change and the consequences for successional pathways has mostly been observed aboveground. Less emphasis has been put on soil microbial communities and their potential effects on plant communities under climate change (Fig. 13.5).

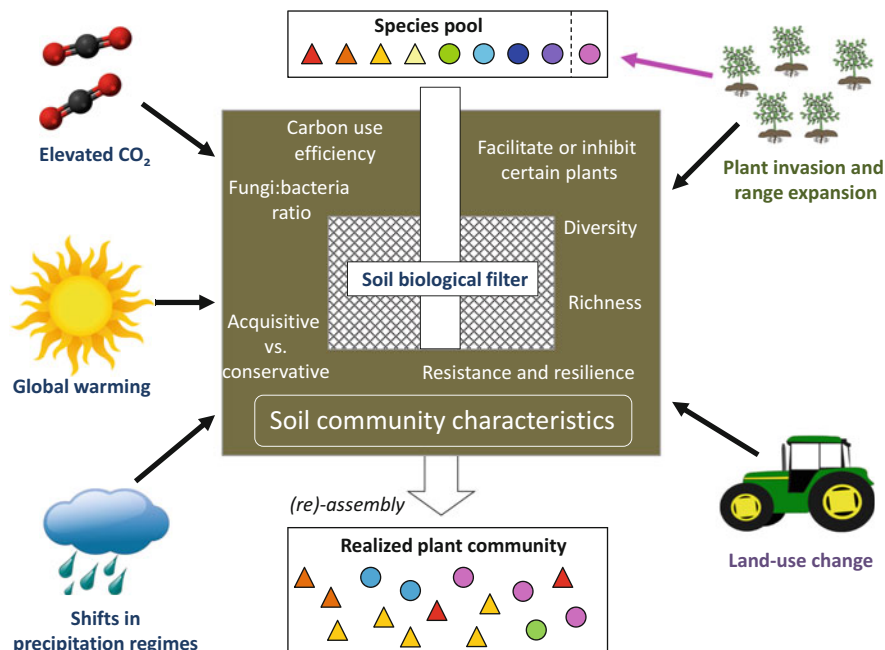


Fig. 13.5 Global and land-use change factors can determine how plant communities assemble and/or reassemble. However, soil biota can impact on *how* these factors affect plant community assembly through a variety of mechanisms. For example, shifts from conservative to acquisitive soil communities as the result of intensive agricultural practices might favor plants with similar (i.e., acquisitive) traits. Further, soil communities that are resistant to changes in precipitation regimes might be better able to buffer the effect of, e.g., drought on the plant community, thereby helping to maintain community diversity. These examples highlight the dynamic, interactive nature between global and land use change, the soil community, and the plant community, pulling focus on the necessity of considering how changes to one component could lead to alterations of the others. To note, plant invasion and range expansion can affect plant community assembly either directly by influencing the species pool (pink arrow) or indirectly through influencing the soil biological filter

What is the role of soil biota in plant community assembly under forecasted climate change perturbations? Soil microbial community composition and biodiversity are being altered by climate change, but evidence suggests that some soil organisms can respond and adapt faster than plants. This may have direct impacts on plant communities. For example, root colonization by mutualistic arbuscular mycorrhizal (AM) fungi often increases under drought, warming, and elevated [CO₂] (e.g., Staddon et al. 2004), thus creating increased resistance and resilience to disturbance for the host plant. A meta-analysis by Augé et al. (2015) suggests that root colonization by AM fungi increased stomatal conductance in plants during water stress, especially under moderate and severe drought. Further, in more than 90% of 32 studies, plant productivity and growth under drought was improved by inoculation with AM fungi (Gehring et al. 2017). Beneficial effects of AM fungi

under drought have implications for plant community composition, particularly when AM fungi form stronger symbioses with some species than others. Mariotte et al. (2017) demonstrated that conservative, subordinate species better resisted drought conditions than acquisitive, dominant species. This was due to the higher degree of mycorrhizal symbiosis of subordinate species, which allowed them to maintain N uptake and increase water use efficiency under reduced water availability. By favoring subordinate species over dominant species under climate change perturbations, AM fungi can, therefore, maintain or increase plant diversity, thereby potentially reducing dominant plant species in the community or even altering succession (Fig. 13.5).

Microbe-mediated effects of climate change on plant communities can also result from changes in decomposer communities, which affects soil C and nutrient cycling. However, it is yet unclear if climate-induced changes in decomposer communities will cause positive or negative effects on plants. So far, studies show variable results. For example, Crowther and Bradford (2013) showed that saprotrophic fungi from temperate woodland soils acclimate to warming by reducing their growth and activity, which would consequently slow down soil organic matter (SOC) decomposition and mineralization. On the other hand, Yuste et al. (2011) showed that, in dry Mediterranean ecosystems, saprotrophic fungi were tolerant to drought and maintained SOC decomposition even under harsh environmental conditions. This suggests that climate change effects on saprotrophic fungi can either reduce or maintain levels of plant-available nutrients. Jassey et al. (2013) showed how climate change effects on saprotrophic microbes can affect plant community assembly. In a warming experiment in peatland, they showed that warming changed the regulatory role of *Sphagnum* polyphenols (i.e., niche modification), which inhibited top predators and promoted bacterial communities. This led to increases in nutrient cycling and increased the abundance of vascular plants at the expense of mosses. Vascular plants produce more easily degradable litter that promotes decomposers, thus potentially creating positive feedbacks that might further accelerate nutrient cycling and shift plant community structure.

In addition, soil nematodes and earthworms help make nutrients available to the plant community through their waste, a function that could be maintained despite forecasted changes in precipitation patterns. Indeed, a recent study showed that nematodes can withstand deep soil frost that occurred due to simulated reduced snow cover meant to mimic climate change-induced shifts in winter precipitation regimes (De Long et al. 2016). Furthermore, Cesarz et al. (2015) found that the negative effects of reduced precipitation on the nematode community were mitigated by increased [CO₂]. This finding demonstrates that interactions between global change factors can cancel out the effects of individual factors, highlighting the need to consider multiple factors in a single experiment. Finally, soil bioturbators have been shown to be particularly resistant and resilient to climatic changes, with their abundance remaining constant or increasing in response to climatic perturbations. For example, earthworms have been shown to increase in abundance under elevated [CO₂] (Milcu et al. 2011). Moreover, Mariotte et al. (2016) showed that the widely dominant earthworm *Lumbricus terrestris* increased in abundance after drought and as such contributed to plant community recovery.

In summary, the effects of the soil biota seem to depend on the type of climate change factor considered (i.e., warming, drought, elevated [CO₂]; see Fig. 13.5). However, interactive effects of multiple climatic factors on soil biota and consequent feedbacks to the plant community remain largely unknown (but see Cesarz et al. 2015). Too often studies evaluated the effects of climate change on plant and soil communities separately and only a few experiments have been aimed at testing how climate change-induced shifts in soil biota affected plant community composition, reassembly, and succession.

13.5.2 Land-Use Change

Land-use intensification and conversion from natural to agricultural land may reduce plant species diversity (Thébault et al. 2014). During the Green Revolution, human-based processes such as deep soil tillage, fertilizer application, and chemical pest control have replaced soil biological processes. Increased physical perturbations, in combination with the expansion of monoculture cropping, have disrupted AM fungal communities and networks (Hamel and Plenchette 2017). Similarly, the abundance and functional diversity of earthworms has strongly declined under agricultural intensification (Chan 2001). This suggests that the role of soil biota in improving plant nutrient uptake (Hamel and Plenchette 2017) and recycling plant inputs and protecting plants against diseases has rapidly decreased (Weller et al. 2002; Pieterse et al. 2014). At the same time, the homogeneous genetic and physical environment of agro-systems (e.g., low plant diversity) has promoted the build-up of new and host-specific soil pathogens (McDonald and Stukenbrock 2016). Furthermore, the reduction in abundance of soil mutualists and bioturbators and the increase in pathogen abundance could ultimately affect the reassembly of plant communities on ex-arable lands (Fig. 13.1), for example through niche modification or by altering species-specific soil–plant interactions.

Can we restore the soil biodiversity in current or ex-arable agricultural systems? The development of AM fungal inoculation technologies suggests that bringing back mycorrhizal-based biological processes is possible. For example, an experiment on chickpeas (*Cicer arietinum*) by Pellegrino and Bedini (2014) demonstrated that inoculation with AM fungi increased crop yield, as well as the nutritional value of the grain. The inoculation of soils with AM fungi can also improve soil fertility by reducing nutrient loss from the soil (Cavagnaro et al. 2015), especially phosphorus and N (van der Heijden 2010). In low-input grasslands or abandoned agro-systems, mycorrhizal-mediated increases in nutrient availability (i.e., increased niche size) could affect plant community reassembly by promoting fast-growing species, similar to how saprotrophs increase nutrient availability and thereby favor fast-growing species (Fig. 13.1b). Van der Heijden et al. (1998) also showed that soil inoculation with a diverse AM fungal community promoted plant diversity because contrasting plant species benefited from different AM fungal taxa. Inoculating ex-arable fields with high diversity mycorrhizal communities could, therefore, encourage the

reassembly of a diverse plant community. Moreover, AM fungal inoculation might both improve the sustainability of crop systems and impact on community reassembly after land abandonment. Additionally, Pieterse et al. (2014) showed that induced systemic resistance might be a mechanism by which plant growth-promoting soil organisms improve defenses against pathogens or root herbivores. For example, they showed that mutualist species of *Bacillus*, *Pseudomonas*, and *Trichoderma* activate the plant immune system, which enhances defense without any cost for the host plant. Additionally, *Fusarium*, *Streptomyces*, and *Actinomyces* can suppress soil pathogens (Weller et al. 2002) through competition for space, hyperparasitism, or antagonism via production of secondary metabolites. Pathogens often build up in crop systems (McDonald and Stukenbrock 2016), and inoculation with disease-suppressive organisms could help restore a more “balanced” soil biotic community composition by limiting the influence of generalist and specialist pathogens (e.g., Fig. 13.1). Therefore, microbial inoculation, alongside increased multispecies intercropping and organic farming practices, could promote plant community diversity in agricultural systems.

Soil biological legacies can last for a long time after abandonment of agricultural practices. For example, Jangid et al. (2011) showed that 17 years after conversion of croplands to grasslands, microbial communities of early-successional grasslands were more similar to microbial communities of the original cropland compared to those of long-term mowed grasslands. This suggests a lasting impact of land-use history on the soil microbial community that continues to affect successive plant communities (de la Peña et al. 2016). Intensive land use generally favors bacterium-dominated communities while reducing the abundance of fungi (e.g., Bardgett et al. 2001; van der Wal et al. 2006). For example, Fraterrigo et al. (2006) showed that 50 years after farming abandonment, soil communities of the recovering forest were still characterized by higher abundance of bacteria and lower abundance of fungi compared to the control unperturbed forest site. Bacterial-dominated soil communities (i.e., low fungal to bacterial ratio) are associated with more rapid decomposition rates and faster nutrient cycling, which promotes N mineralization (Wardle et al. 2004; de Vries et al. 2013). A lasting reduction in the soil fungal to bacterial ratio after cessation of agricultural activities is, therefore, expected to favor resource-acquisitive plant species over conservative species (Fig. 13.1c; Grigulis et al. 2013), thus increasing plant dominance and productivity while reducing diversity. Agricultural soil legacies can also have strong impacts on the assembly of the recovering vegetation by differentially affecting the success of early-colonizing species (Kardol et al. 2007; Bauman et al. 2013) (see Sect. 3.2). However, it is important to note that management practices related to land use do not always have major impacts on the soil biota and subsequently plant community assembly. For example, it has been shown that regular clear cut harvests reduced the diversity of EM communities but did not affect the growth of regenerating tree seedlings and, thus, did not affect community succession toward mature forests (Kranabetter 2004).

Overall, intensification and land-use change are largely responsible for the loss of soil biota diversity in agro-systems, creating soil legacies that continue to affect plant communities long after land-use abandonment. Certain management practices can

mediate negative effects of land-use change on soil biota. Recent research also suggests that soil biota-based technologies (e.g., AM fungi inoculants) can contribute to more sustainable agricultural practices (e.g., Cavagnaro et al. 2015). Moreover, soil inoculation with soil mutualists and disease-suppressive organisms could help counterbalance soil legacies after land-use abandonment, through niche modification, specific effects on pathogens, and improved plant resistance. Finally, adopting practices such as no/low-till agriculture, multispecies intercropping, and natural pest management will also help restore soil community function and diversity, with knock-on effects for plant community reassembly (Fig. 13.5).

13.6 Synthesis and the Way Forward

In this chapter, we explored how soil biota drive plant community assembly through niche modification and through soil legacies. Effects of soil biota on plant performance have been studied intensively (e.g., Wardle et al. 2004), but our understanding of how soil biota affect the processes by which plant species are filtered from the species pool into local communities is still limited. As we discussed in this chapter, this understanding can help us predict how plant communities reassemble under altered land use, climatic change, and plant invasion. This will further allow us to develop strategies for ecosystem restoration and conservation.

Where to go from here?—A major challenge in studying the effects of soil biota in plant community assembly is our limited knowledge of the ecology of soil biota. Novel developments in the analyses of soil communities promise to provide new insights into the enormous genetic and taxonomic diversity belowground and the divergent niches occupied by soil biota (e.g., Taylor et al. 2014). However, in addition to molecular sequencing, we advocate prioritizing empirical studies manipulating the order and timing of plant species arrival (or, in case of eradication of invasive plants, the order of species removal) in combination with varying the composition of soil communities. Such experiments would benefit from trait-based approaches which are now common in plant ecology (van Kleunen et al. 2010), but still in the early stages of development when it comes to soil biota (e.g., George and Lindo 2015; Widenfalk et al. 2016). Further work needs to be done, but such trait-based approaches should also help in teasing apart the relative contribution of different groups of soil organisms, e.g., mutualists versus pathogens.

A further challenge lies in actively using soil biota (e.g., microbial inocula) for sustainable agricultural practices, restoring and conserving endangered plant communities, and combating the effects of climatic change and plant invasions. Accounting for interactions between different global change factors that simultaneously affect plant and soil communities when designing experiments will enhance the real-life applicability of the results obtained (Kardol et al. 2012). So far, most experiments testing the effects of soil biota on plant community assembly have been run under controlled (i.e., greenhouse) conditions. Therefore, our knowledge on the relative importance of soil biota and how their effects vary in relation to

environmental factors is still limited. Field experiments manipulating soil biota come with their own challenges, but are nevertheless valuable due to an added sense of realism. Alternative approaches would include controlled experiments using larger mesocosms and adding environmental manipulations (e.g., soil chemistry or climate) to the experimental design. Future studies should also focus on the importance of local and regional species pools (both for plant and soil organisms) and how community membership depends on dispersal.

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