Plant-soil feedbacks and temporal dynamics of plant diversity-productivity relationships

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Abstract

Plant-soil feedbacks and diversity-productivity relationships are important research fields to study drivers and consequences of changes in plant biodiversity. While studies suggest that positive plant diversity-productivity relationships can be explained by variation in plant-soil feedbacks in diverse plant communities, key questions on their temporal relationships remain unaddressed. Here, we discuss three processes that change plant-soil feedbacks over time in diverse plant communities, and their effects on temporal dynamics of diversity-productivity relationships: 1) spatial redistribution and changes in dominance of plant species, 2) phenotypic shifts in plant traits, and 3) dilution of soil pathogens and increase in soil mutualists. Disentangling these processes in plant diversity experiments will yield new insights into how plant diversity-productivity relationships change over time.

Keywords: *biodiversity-ecosystem functioning; plant-soil interactions; spatial turnover; trait evolution; dilution effects*

Plant-soil feedback and biodiversity-ecosystem functioning research

In the 1990s, two independent fields of plant ecology research began to provide new insights into causes and consequence of plant diversity in terrestrial grassland ecosystems. The first, plant-soil feedback (PSF) research (Box I), aims to investigate how interactions of plants with biotic and abiotic soil conditions affect their own growth and performance, as well as that of conspecific and heterospecific plant “successors” in the community [1,2]. In the last two decades, PSF research has shown that negative conspecific PSFs can play an important role in maintaining plant diversity, and that shifts in the strength of PSF over time can be associated with shifts in plant community composition [1–5]. The second, (plant) biodiversity-ecosystem functioning (BEF) research, primarily aims to establish a causal link between plant diversity loss and ecosystem functioning, often measured as primary production (i.e. the diversity-productivity relationship; [6]). Experimental BEF research (Box II) has shown that primary production is on average higher in plant communities with a greater number of plant species, although the relationship usually saturates beyond a certain threshold [6,7]. An important observation is that these positive plant diversity-productivity relationships usually become stronger over time, at least in grassland ecosystems [8,9]. Yet, the underlying ecological and evolutionary mechanisms that strengthen (or weaken) temporal plant diversity-productivity relationships remain poorly understood [6,10]. In this review, we discuss how emerging insights from PSF research can be integrated into BEF research for a better understanding of temporal dynamics of plant diversity-productivity relationships.

Box I: Plant-soil feedback

Plant-soil feedback is the effect of one plant species, via its influence on the soil, on the performance of the same species or a different species [1]*. The first plant influences or "conditions" the soil by changing the soil microbial community and/or the soil abiotic conditions, such as the presence of allelochemicals, nutrient availability, moisture, and structure, in a specific manner. If the second plant grows worse in the conditioned soil, relative to its growth in another soil, e.g., soil conditioned by a different species, the plant exhibits a "negative feedback" while for the reverse situation this is called "positive feedback". When the responding plant grows differently on soil conditioned by the same species, the feedback is called a "conspecific feedback", and there is a "heterospecific feedback", when the conditioning and responding (feedback phase) plants belong to different species. The sensitivity of a plant to changes in the soil caused by other conspecific or heterospecific plants can vary greatly among species, but overall, the majority of grassland species exhibit a negative conspecific feedback* [11]*. Some key trait differences between the two types of feedback species (i.e., positive and negative) are illustrated in figure I. Plant-soil feedback effects are particularly important for establishing seedlings in the field* [12]*. Moreover, in the field, soil legacies of previous plants can be detected even in the succeeding growing season* [13]*.*

Box II: Plant BEF experiments

Plant BEF experiments principally aim to understand the effects of plant diversity loss on ecosystem functions, such as primary production, nutrient cycling, energy fluxes to higher trophic levels [6]. The earliest plant BEF experiments were assembly experiments and involved sowing different randomly assigned numbers and

combinations of plant species into plots. These experiments created plots with a gradient of plant diversity ranging from monocultures (with only 1 species) to polycultures (mixtures), containing two to usually around 20 species (occasionally more). Species compositions are randomly selected from a larger pool of co-occurring species, in order to prevent any confounding between composition and species richness. Almost all such BEF experiments are weeded to remove incoming plant species and to maintain the diversity gradient established at the start of the experiment, however, sown plant species can go locally extinct in longer-running BEF experiments and species abundances can greatly shift over time [14]. A few BEF experiments used a removal approach, where plant species are manually removed from communities to simulate extinctions [15,16]. The early BEF experiments were all done in grasslands, but an increasing number of experiments have also been established in forests [17]. Recently, there has been an increased interest in transferring the results of BEF experiments to real world situations, to study realistic patterns of diversity change. In real-world BEF studies, abiotic conditions may also affect ecosystem functioning and species assemblages are non-random and correlated with diversity. Such studies therefore aim to determine the importance of diversity changes alongside these other factors [18].

Temporal changes in plant diversity-productivity relationships

Several field experiments have shown that plant diversity-productivity relationships become more positive over time [8,9,19,20]. Two phenomena have been suggested to contribute to this pattern [6,21]: First, the productivity of many diverse plant communities increases over time [9,22] and second, some monocultures become less productive over time [8,19]. While evidence for the underlying mechanisms driving these two

phenomena is still scarce, BEF researchers have suggested that an increase in niche differentiation (e.g., *via* resource partitioning) in diverse plant communities may drive an increase in mixture performance over time [6,9]; although what exactly drives such observed increase in temporal niche differentiation among plants remains poorly understood. Alternatively, reduced performance of monocultures over time could be due to an increase in pathogenic soil microorganisms or nematodes that infect or feed on plant roots [23,24]. Many of these plant enemies, such as pathogenic fungi, are specialized on particular host plants and become increasingly abundant in their host plant monocultures [25,26]. Accumulation of these antagonists over time in monocultures, could therefore cause a progressive decline in monoculture biomass relative to biomass of diverse plant communities [23,27].

BEF researchers have repeatedly called for investigations into the processes that operate in diverse plant communities to enhance their performance relative to monocultures [28,29]. For instance, biotic feedbacks between plants and other trophic levels (e.g., soil microorganisms or aboveground herbivores) could be important drivers of biomass production in species-rich plant communities [29]. We know little, however, about how exclusive these processes are to species-rich plant communities, how they change over time, and how such temporal changes may strengthen (or weaken) the productivity of diverse plant communities [10,22,23,29]. Among several biotic feedbacks that can be identified in species-rich plant communities [29], we here focus on temporal shifts in plant-soil feedbacks in species-rich plant communities (Box I).

Temporal changes in plant-soil feedbacks in diverse plant communities

As revealed by PSF experiments, many grassland plant species experience some degree of negative conspecific feedback [11,30] (Box I, Figure I). The progressive decline in productivity in certain plant monocultures could very well relate to increasing negative conspecific feedbacks over time driven by the accumulation of (host-specific) pathogens in the soil (Figure 1). The PSF concepts are more challenging to apply to diverse plant communities as both conspecific and heterospecific PSFs simultaneously occur in diverse plant communities [30,31]. Heterospecific feedbacks are particularly difficult to predict as the response of an individual plant species to the soil in which another species has previously grown is likely to depend on the identity of both the first and the second ('successor') species (Box I) [32]. However, studies have shown that grasses and forbs generally grow better in soils previously conditioned by species from a different functional group [13,30,33]. Moreover, closely related plant species (i.e. species having a low phylogenetic distance) exert greater negative heterospecific feedback than distantly related plants mainly because the likelihood for soil pathogens to infect other plants is higher when the plants are phylogenetically related to the host plant [5,34,35]. The factors that can predict the magnitude and direction of conspecific and heterospecific feedbacks in diverse plant communities are therefore essential ingredients for incorporating PSF knowledge into BEF research.

Building upon advances in how plant-soil feedbacks may operate in diverse plant communities [31,36], and how plant-soil feedbacks can be predicted in the field [13,37], we highlight three processes that occur in species-rich plant communities and can help understand the temporal dynamics of diversity- productivity relationships (Figure 2): 1)

Spatial plant redistribution and local changes in plant abundance, 2) Phenotypic shifts in plant traits, and 3) Changes in the soil biotic community, in particular, a dilution of pathogenic soil biota and an increase in plant-mutualistic soil biota. We highlight that when these three temporal processes contribute to reducing negative feedbacks in diverse plant communities, the productivity would increase over time. We discuss these processes in the context of BEF experiments and how they help us understand temporal patterns of productivity in real -world BEF studies (Box II).

Spatial redistribution and shifts in abundance

Several grassland plants overcome conspecific negative feedbacks by shifting their local spatial distribution, and so they occupy different soil patches over time [38,39]. Such a response usually reduces the accumulation of specialized soil-borne pathogens on a given host plant at a given location [40,41]. In monoculture plots, the spatial redistribution of plant individuals is obviously less effective in terms of pathogen evasion, unless there are many open patches previously unoccupied by a given plant species. Spatial redistribution is expected to be more common for species with strongly negative conspecific feedbacks (Box I, Figure I) than for species with neutral or positive feedbacks (Figure 1) [42]. This prediction could be tested with data from biodiversity experiments where the spatial distribution (or turnover) of species is recorded over time, e.g., in permanent quadrats in each plot.

In a diverse plant-community, individuals of plant species experiencing negative conspecific feedbacks can escape their pathogens by dispersing to new patches previously occupied by a plant of a different species. The key assumption here is that

the soil pathogens (associated with the previously present plant) do not exert a strong negative effect on the new colonizing plant [11,37,43,44]. The spatial range of soil pathogen effects is also assumed to be small; although empirical evidence of this remains scarce, experiments have shown that spatial heterogeneity of soil biota regulates PSF [45–47]. Within a high diversity plot, however, the extent of heterospecific feedbacks that arise by spatial shuffling will likely vary depending on the functional difference (traits and/or groups) and phylogenetic distance of the neighbours to the newly colonizing species. These variable heterospecific feedbacks subsequently increase the temporal and spatial variation in the abundance of species, and such variation should be the highest in plots which are functionally and phylogenetically diverse.

The temporal diversity-productivity relationship is often argued to depend on environmental fluctuations over time [48,49]. Although these fluctuations are assumed to be largely driven by exogenous environmental conditions [48], the biotic interactions between neighbouring plant species, such as *via* soil organisms, could influence temporal variation in plant abundance. Estimating the shifts in PSF during the spatial redistribution of plant individuals in diverse plant communities can help provide insight into how intrinsic biotic factors influence temporal (a)synchrony in species-specific biomass or abundance. For instance, soils from patches where spatial plant redistribution is higher can have different PSF on component plants than soils where spatial redistribution is lower. These patch-specific differences in PSF can be linked to variation in temporal (a)synchrony of plants in species-rich communities. Further, whether shifts in PSF, *via* spatial redistribution, increase complementarity among species (e.g., in resource use) and thereby plant biomass production in species-rich

communities over time merits both theoretical (e.g., simulation studies) and experimental scrutiny. A recent greenhouse study that estimated the strength of PSF using soils from a three-decade-old plant monitoring field study, reported that plant species experiencing greater negative conspecific feedbacks were also temporally more variable in their field abundances [44]. It will be further important to examine the relationship among the extent of spatial redistribution, the magnitude of temporal (a)synchrony in plant biomass/abundance and the strength of PSF for plant species of diverse communities through simulation and empirical studies, and whether changes in this relationship can help explain temporal dynamics of diversity-productivity relationship.

Phenotypic shifts in plant traits

Traits of plants from species-rich communities are often more variable than those from the same plant species growing in their respective monocultures [50]. This is particularly true for traits related to (interspecific) competition, such as specific leaf area and plant height, which are crucial for resource acquisition [50]. We can expect that selection for competition-related traits in mixed plant communities can enhance trait divergence thereby enhancing the complementary use of limited resources [50,51]. We propose that shifts in competition-related traits in a plant also affect the strength of plant-soil feedbacks as plant traits are often associated to how they affect soil biotic and abiotic environments [52]. That is, if a species with negative feedback exhibits greater divergence in its competition-related traits from its neighbouring species, we could also expect divergence in how the two species will influence their local soil environment and thereby their effects on both conspecific and heterospecific plants. For instance, root

traits affecting plant competition for soil resources, such as specific root length [53,54] can alter the strength of PSF [55]. Temporal divergence in competition-related traits in diverse plant communities could help explain temporal strengthening of diversity-productivity relationships if such trait-divergence results in a reduction of the strength of negative PSF over time.

Shifts in competition-related plant traits in diverse plant communities have mainly been demonstrated for aboveground plant traits [50] (Figure 2). Even though selective pressure for divergence in aboveground competition-related traits is weakly linked to soil microorganisms in diverse plant communities, it can be related with variation in plant defence traits in monocultures [56]. Indeed, selection for traits related to defence against pathogens can be expected to be higher in monocultures due to the absence of interspecific competition and a greater probability of host-specific pathogen accumulation [50,56]. Given the role of root traits in acquiring limited resources [57], divergent selection in root traits over time in diverse plant communities can occur, and thereby contribute to niche differentiation for resource acquisition. However, whether temporal shifts in the strength of plant-soil feedback due to spatial redistribution (and changes in plant abundance) could affect the selective environment for above- and belowground plant traits remain virtually unexplored. This line of inquiry is important though, as the biotic neighbourhood is a crucial determinant of phenotypic plasticity in plants [58].

Trait evolution in diverse plant communities is not only limited to competition- and defence-related traits but also to life-history traits. A recent study showed that the

219 longevity of a plant species growing in a diverse plant community increased, while its
220 reproduction was delayed [59]. Examining the effects of trait evolution on PSF in long-
221 running plant diversity experiments can unravel how evolutionary processes can explain
222 temporal diversity-productivity relationships. Currently, there is a growing interest in
223 applying the principles of eco-evolutionary feedbacks to both BEF and PSF research
224 [60,61]. In line with these trends, our current understanding of character displacement in
225 competition-related traits in long-running biodiversity experiments can be extended to
226 other traits and could provide an important basis for investigating how divergent
227 selection for niche differentiation both drives, and is driven by PSF. Conversely, if trait
228 evolution in plants promotes positive PSF for certain plant species, productivity in
229 diverse plant communities can still increase due to the presence of high biomass plant
230 species [62] (also referred as positive selection effect [63]). We suggest that a better
231 understanding of PSF in relation to both competition- and defence-related plant traits
232 above- and belowground in diverse plant communities is a key step to obtain a
233 mechanistic understanding of temporal diversity-productivity relationships [64,65].

234

235 *Dilution of soil pathogens and increase in soil mutualists*

236 Epidemiological studies have long shown that diversity slows the spread of diseases
237 due to greater dilution of pathogens [66,67]. A dilution of pathogens essentially means
238 that their net effect on potential hosts decreases. This occurs through several
239 mechanisms, including effects of other species on trophic regulation of the pathogens
240 by their predators, reduced transmission, or a decrease in host quality [68,69].
241 Therefore, pathogen dilution would result in a reduction of negative plant-soil feedbacks.
242 The dilution of soil fungal pathogens was recently demonstrated in a plant-diversity

experiment, where more than 50% of pathogenic fungal operational taxonomic units (OTUs) found in monocultures were absent from diverse plant communities, composed of the same plant species [25]. The exact mechanism by which pathogen dilution occurs in diverse plant communities, and particularly in long-running diversity experiments, is still poorly understood. The general notion is that pathogen specialization on a given host plant is constrained in a multi-plant environment [23,70]. Trophic control of fungal or other plant pathogens in the soil is another mechanism underlying pathogen dilution, as diverse plant communities can sustain a greater density and diversity of microbial predators than plant monocultures [36,71,72].

Soil-microbial diversity and biomass increase in plots with a high diversity of plants in field experiments [73,74]. If a temporal increase in microbial diversity and biomass in diverse plant communities is due to a relative increase in mutualistic microorganisms (e.g. saprotrophic fungi, mycorrhizal fungi) over pathogenic microorganisms [27], this would further reduce the strength of negative feedback experienced by plants [75]. Interestingly, it also raises the question of whether the relative decline in plant pathogens in diverse plant communities will eventually decrease the need for the continuous spatial redistribution of plant individuals of negative feedback species. We might therefore expect a temporal saturation in spatial redistribution (or turnover) over time in diverse plots (where the diversity gradient is maintained) whereas in diversity experiments in natural grasslands where colonization of non-sown plants is allowed, saturation might be less likely as newly colonizing plant species would continue to perturb the pathogen dynamics [76,77].

Plant-soil feedbacks can also vary due to plant mutualists in the soil that benefit plants by acquiring nutrients or suppressing pathogens [78,79] (Figure 1). For instance, a greater diversity of mutualistic soil microorganisms decreases the strength of negative plant soil-feedbacks [75,80]. Following a disturbance (which occurs at the establishment of the experiment), both the diversity and the density of plant-beneficial microorganisms and soil invertebrates increase over time, but this increase is typically stronger in diverse communities than in monocultures [27]. The association of a plant with mutualists such as arbuscular mycorrhizal fungi in diverse plant communities can also drive phenotypic divergence in plant competition-related traits [56,81]. If such soil-microbe-driven plant-trait variation reduces negative plant-soil feedback, productivity is likely to increase in diverse plant communities over time.

Some monocultures or low-diverse plant communities can be productive over longer time periods. Plants in these plots accumulate mutualists, because of their positive PSF (Box I, Figure I). Such positive mutualist effects can also negatively influence species diversity in species-rich communities as greater mutualist accumulation can promote the dominance of few selective plants [82]. We still poorly understand how mutualist accumulation in high and low diverse plant communities affects respective temporal (a)synchrony in plant specific biomasses. For instance, how does mutualist accumulation in positive-feedback species (Figure 1) vary between low- and high diverse plant communities, and how would this affect the temporal dynamics of diversity-productivity relationships (see Outstanding Questions). Temporal variation in trophic regulation of soil pathogen and mutualist may further affect pathogen dilution and/or mutualist accumulation [83]. Indeed, the temporal shifts in PSF eventually will depend on how the relationship between the plant and its pathogens, and mutualists

changes over time, as the direction and strength of feedback is often the net sum of negative and positive effects from soil biota [1].

Applications in real-world ecosystems

A key question that needs further attention, in order to integrate PSF and BEF research, is how the three temporal processes we discussed operate in real-world ecosystems (Box II) [84]. The heterogeneous colonization patterns of plants in real-world ecosystems makes them temporally more dynamic (i.e., there is greater spatio-temporal turnover of plant species including changes in species richness) in these systems than in many long-running BEF experiments [85]. Real-world ecosystem studies have shown that greater plant diversity also leads to increased plant-biomass production among other ecosystem functions [18,85]. In real-world ecosystems, plant identity will likely play an important role in determining how the three processes develop and contribute to temporal strengthening (or weakening) of BEF relationships. For instance, colonization by exotic plants and their population explosion can suppress native species with negative feedbacks [5,86,87]. This will simultaneously affect the number of species in diverse plant communities (due to the local competitive exclusion of native plants) and subsequently the three temporal processes that change PSF. Soil collected from diversity experiments of various establishment ages can be used to test this hypothesis by introducing exotic plants and thereby examining how feedbacks of native plant species shift in the presence of exotic plants.

Outlook

Both PSF and BEF research have yielded mechanistic insights into the causes and consequences of plant diversity in terrestrial ecosystems [1,6]. We suggest that to understand temporal variation in the effects of plant diversity on plant productivity, we require insights into the processes that cause spatial and temporal shifts in PSF in diverse plant communities. While our conceptual framework is mainly based on grassland plants, we assume that processes like spatial plant redistribution, their trait evolution, and pathogen dilution or mutualist accumulation in soils may also operate in other ecosystems, such as in forests. It will be interesting to examine how the relative importance of these three processes may differ between grasslands and forests to influence temporal diversity-productivity relationships *via* temporal changes in plant-soil feedbacks, given that the temporal strengthening of diversity-productivity relationship has also been shown in forest ecosystems [22].

The three processes discussed here (Figure 2) are certainly not exhaustive, as many other processes can also contribute to temporal variation in diversity effects on plant productivity. In fact, it is likely that many other biotic (and abiotic) factors, such as aboveground grazing of plants by herbivores will perturb these three temporal processes, and thereby increase or decrease the strength of PSF. For instance, there is increasing evidence that aboveground herbivory by insects and mammals affects the functioning of soil microbial communities [88,89], and therefore potentially the magnitude and direction of PSF. For instance, functional shifts in soil microbial communities could potentially affect the temporal build-up of the dilution effect in diverse plant communities. Aboveground herbivores can further reduce the plant's investment in competition-related traits over defence- and/or tolerance-related traits [90,91], and thereby affect trait evolution and PSF relationships [92]. Herbivory can also shift the

competitive (a)symmetry among neighbouring plants, and this, in turn, can have consequences for the temporal shifts in PSF [93–95], such as through changes in PSF *via* the traits of competitively superior plants.

Stochastic disturbances such as climate change-induced droughts or floods also alter the temporal dynamics of (plant) diversity effects. We still know little about how such stochastic disturbances alter the processes through which temporal PSF influence the performance of plants in diverse plant communities. These disturbances can alter the proposed three processes by either reducing plant diversity or by affecting other biotic components, such as soil microorganisms through abiotic stress. While there is some evidence that diverse plant communities exhibit greater resistance to particular stochastic disturbances [96–98], there is an urgent need for research that can disentangle how such disturbances alter the role of PSFs in influencing the temporal dynamics of plant productivity in diverse plant communities.

Concluding remarks

We conclude that temporal variation in plant diversity and productivity relationships is likely related to spatial redistribution of plants (and changes in their abundance), phenotypic shifts in competitive plant traits and soil pathogen dilution (supplemented by soil mutualist accumulation). These processes reduce the strength of negative PSF in diverse plant communities, and thereby strengthens the diversity-productivity relationship over time and causes PSF, particularly for negative feedback species, to vary from year to year which might promote temporal niche partitioning in diverse plant communities [99,100]. We further advocate for combining ecological (e.g., spatial

processes) and evolutionary (e.g., trait evolution) approaches to help integrating PSF and BEF research, which is a promising avenue for generating new mechanistic insights into the causes and consequences of plant diversity (see Outstanding Questions).

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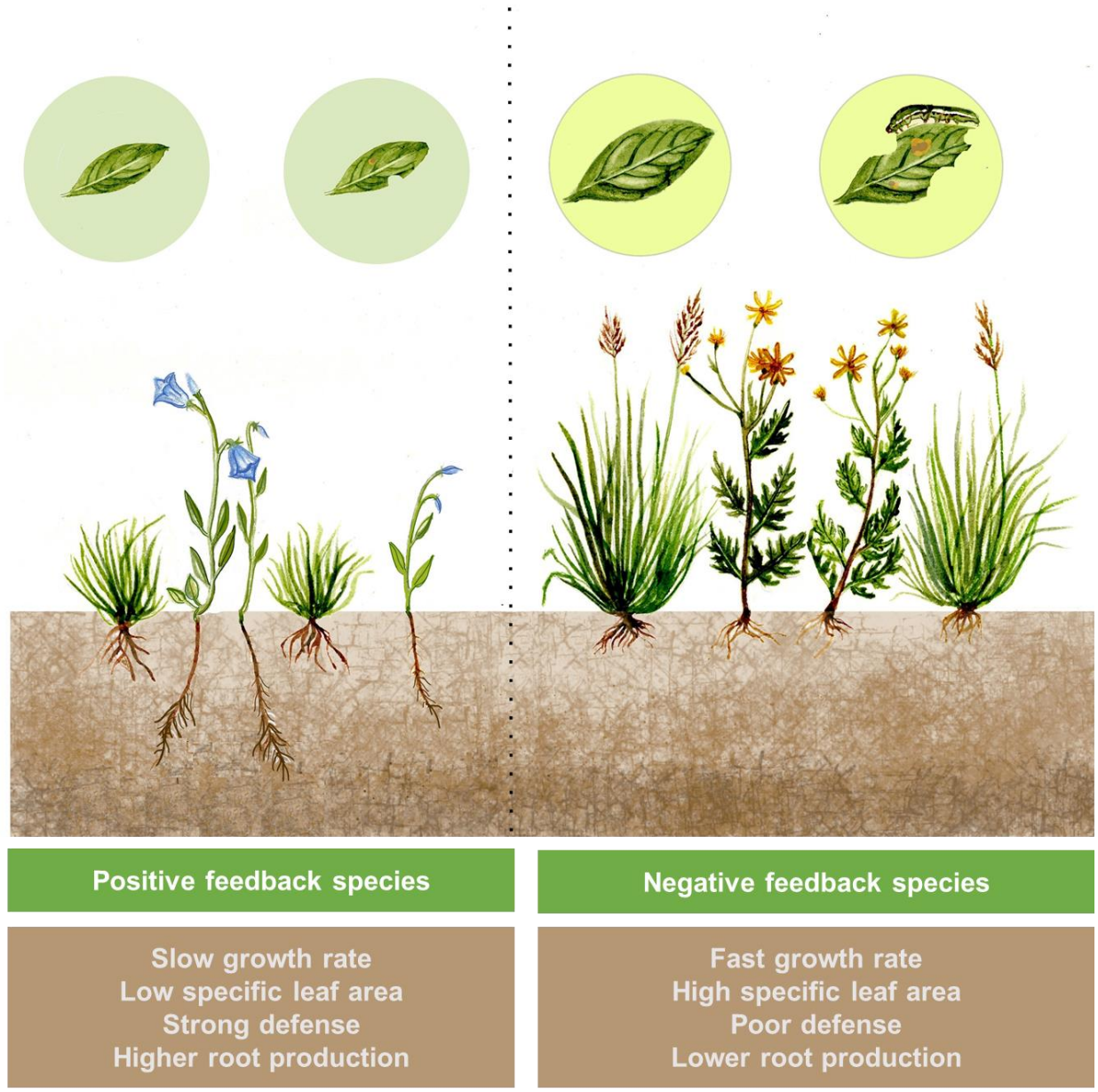

Figure I (Box I): Common differences between plant species that experience positive and negative plant-soil feedback. When we refer to a species as a positive or a negative feedback species, we refer to its conspecific plant-soil feedback.

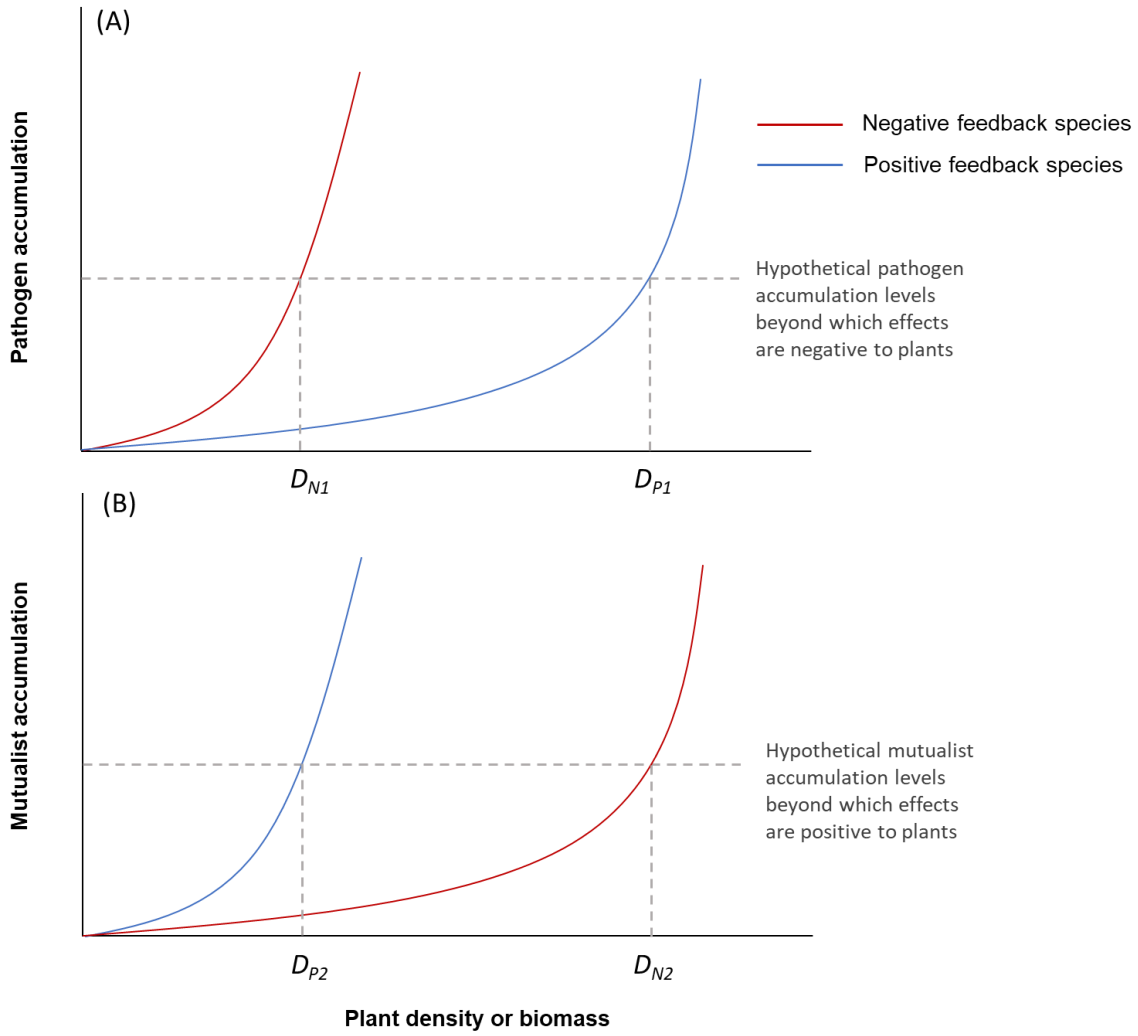

Figure 1: Temporal accumulation of (A) soil pathogens and (B) soil mutualists may vary between positive feedback and negative feedback species, which is often driven by plant density or biomass. A negative feedback species is already experiencing negative pathogen effects at low densities (D_{N1} in panel A), whereas a positive feedback species benefits from mutualist effects at low densities (D_{P2} in panel B). In contrast, a negative feedback species needs to reach a higher density to benefit from mutualists (D_{N2} in panel B), whereas positive feedback species suffer from pathogens at high densities (D_{P1} in panel A). The time to reach D_{N1} or D_{P1} is less than the time to reach D_{N2} or D_{P2}. Note that pathogen and mutualist accumulation curves will saturate at some point in time (not shown in the figure) depending on density-dependence in pathogens and mutualists, and also on the density or biomass of host plants.

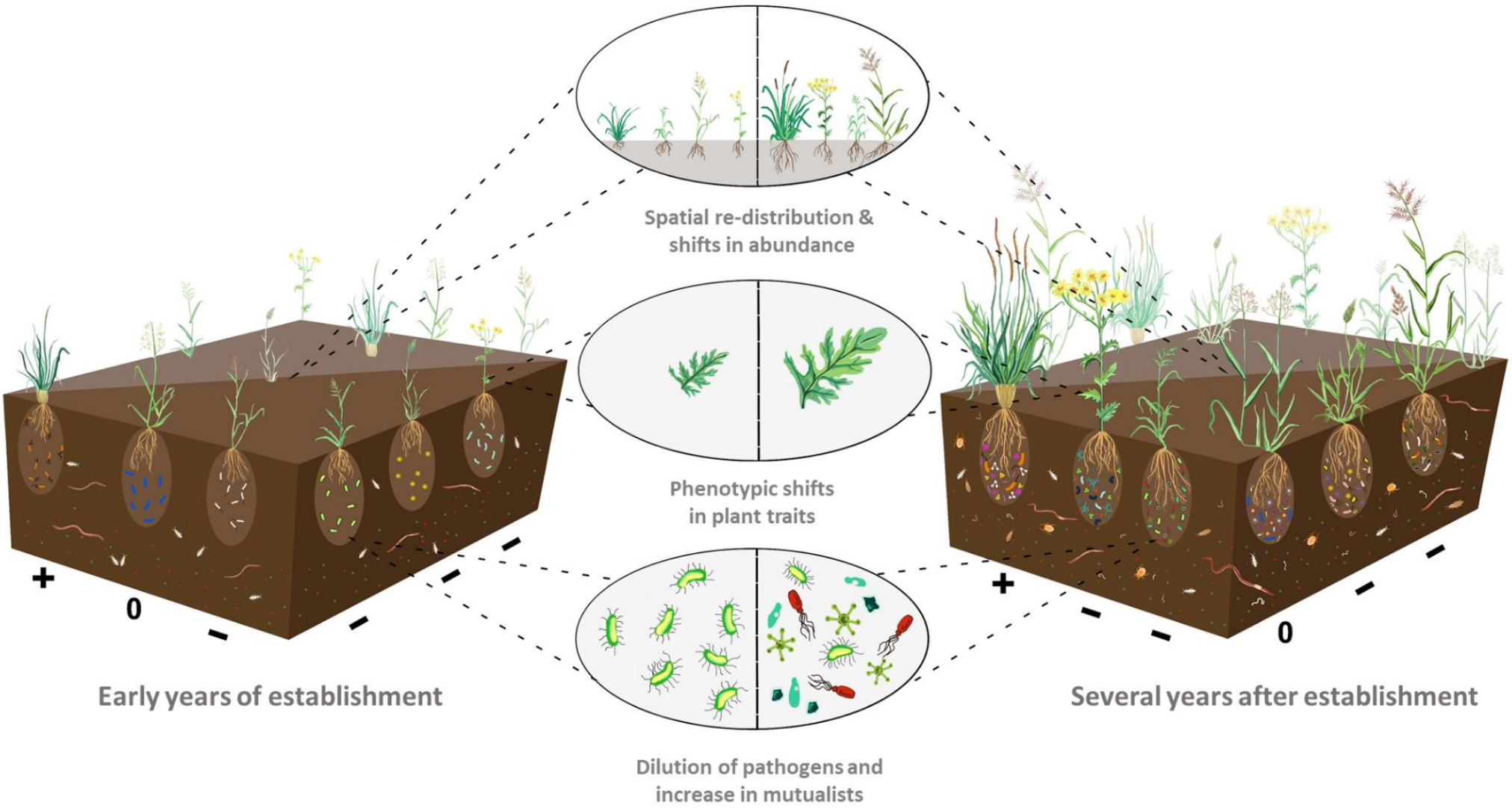
Spatial re-distribution &
shifts in abundance
Phenotypic shifts
in plant traits
Dilution of pathogens and
increase in mutualists
+
0
−
+
−
−
0
Early years of establishment
Several years after establishment

Figure 2: Plant-soil feedbacks will change over time in diverse plant communities. After several years, plant-soil feedbacks in diverse plant communities change mainly via three non-mutually exclusive temporal processes: spatial re-distribution and changes in abundance (mainly of negative feedback) of plant species, phenotypic shifts in plant traits (e.g., resource acquisition traits like surface leaf area or specific root length in a plant species), and dilution of pathogens (e.g., pathogenic fungi) and increase in mutualists (e.g., arbuscular mycorrhiza). Feedback characteristics of a plant are shown by +, 0 and – signs. Spatial redistribution is shown via spatial rearrangement of plant species. Changes in abundance is shown by the size of the plants. Phenotypic shifts in plant traits are shown via changes in the size of plant organs (e.g., leaf size). Dilution effects of pathogens and increase in mutualist biota are shown *via* a greater variety of soil biota.