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

Thakur, M.P.; Putten, W.H. van der; Wilschut, R.A.; Veen, G.F.; Kardol, P.; Ruijven, J. van; … ; Bezemer, T.M.

Citation

Thakur, M. P., Putten, W. H. van der, Wilschut, R. A., Veen, G. F., Kardol, P., Ruijven, J. van, … Bezemer, T. M. (2021). Plant-soil feedbacks and temporal dynamics of plant diversity-productivity relationships. *Trends In Ecology & Evolution*, *36*(7), 651-661. doi:10.1016/j.tree.2021.03.011

Trends in
Ecology & Evolution

CellPress

Review

Plant–Soil Feedbacks and Temporal Dynamics of Plant Diversity–Productivity Relationships

Madhav P. Thakur,[1,*] Wim H. van der Putten,[2,3] Rutger A. Wilschut,[4] G.F. (Ciska) Veen,[2] Paul Kardol,[5] Jasper van Ruijven,[6] Eric Allan,[7] Christiane Roscher,[8,9] Mark van Kleunen,[4,10] and T. Martijn Bezemer[2,11]

Plant–soil feedback (PSF) 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 PSF in diverse plant communities, key questions on their temporal relationships remain. Here, we discuss three processes that change PSF over time in diverse plant communities, and their effects on temporal dynamics of diversity–productivity relationships: spatial redistribution and changes in dominance of plant species; phenotypic shifts in plant traits; and 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.

Highlights

Plant diversity–productivity relationships often become stronger over time, but we know little about what biotic mechanisms may drive temporal dynamics of diversity–productivity relationships.

Recent advances in plant-soil feedback (PSF) research can help gain new mechanistic insights into temporal dynamics of diversity–productivity relationships.

We suggest three processes driving temporal changes in PSF of individual plants in diverse plant communities: spatial redistribution and changes in the dominance of plant species; phenotypic shifts in plant traits; and dilution of soil pathogens and increase in soil mutualists.

These three processes reduce the strength of negative feedback in the absence of external disturbances and make diverse plant communities more productive over time.

Plant–Soil Feedback and Biodiversity–Ecosystem Functioning Research

During the 1990s, two independent fields of plant ecology research began to provide new insights into the causes and consequence of plant diversity in terrestrial grassland ecosystems. The first, PSF research (Box 1), 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]. Over the past two decades, PSF research has shown that negative conspecific PSFs can have 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 2) 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.

Temporal Changes in Plant Diversity–Productivity Relationships

Several field experiments have shown that plant diversity–productivity relationships become more positive over time [8,9,11,12]. Two phenomena have been suggested to contribute to this pattern [6,13]: first, the productivity of many diverse plant communities increases over time [9,14]; and second, some monocultures become less productive over time [8,11]. While evidence for the underlying mechanisms driving these two phenomena remains scarce, BEF researchers have suggested that an increase in niche differentiation (e.g., via resource partitioning) in diverse plant communities drives an increase in mixture performance over time [6,9], although what

[1]Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland
[2]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO- KNAW), Wageningen, The Netherlands
[3]Laboratory of Nematology, Wageningen University, Wageningen, The Netherlands
[4]Ecology, Department of Biology, University of Konstanz, 78464, Konstanz, Germany
[5]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden
[6]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands
[7]Institute of Plant Sciences, University of Bern, Bern, Switzerland

Box 1. Plant–Soil Feedback

PSF 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 'conspecific feedback', and 'heterospecific feedback' occurs when the conditioning and responding (feedback phase) plants belong to different species. The sensitivity of a plant to changes in the soil caused by conspecific or heterospecific plants can vary among species, but overall, most grassland species exhibit a negative conspecific feedback [22]. Some key trait differences between the two types of feedback species (i.e., positive and negative) are illustrated in Figure I. PSF effects are particularly important for establishing seedlings in the field [96]. Moreover, in the field, soil legacies of previous plants can be detected even in the succeeding growing season [26].

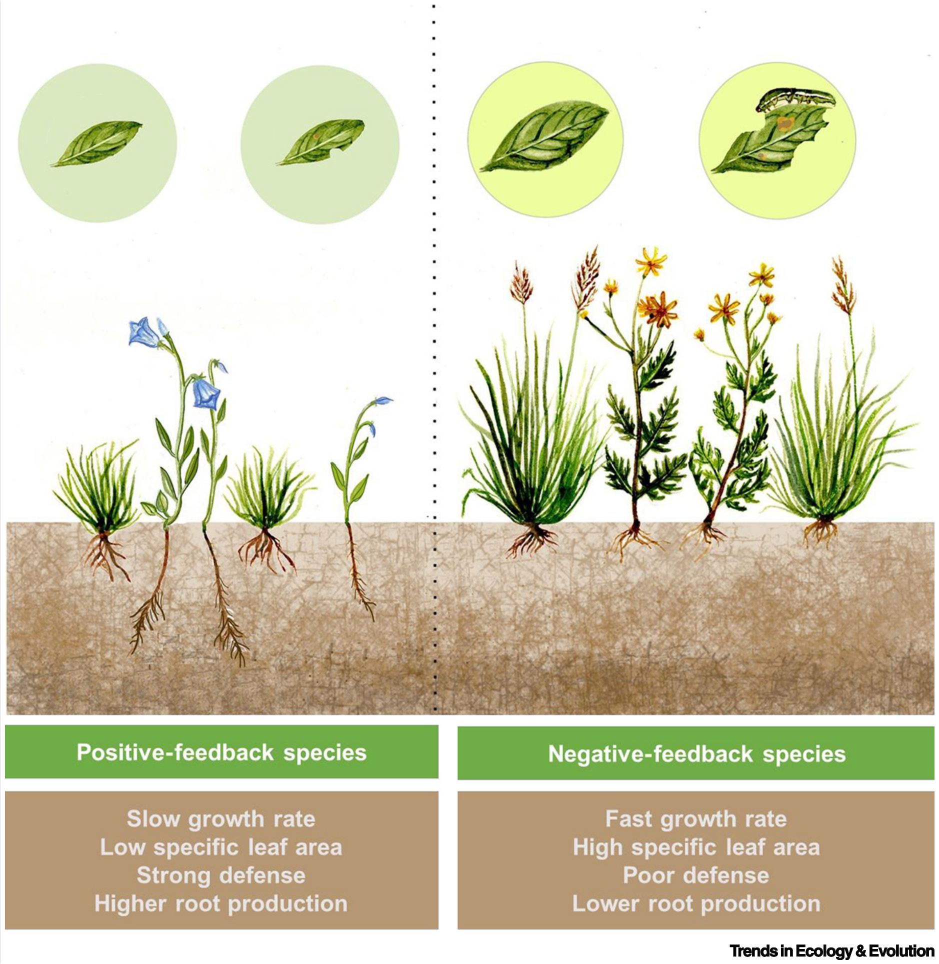


Figure I. Common Differences between Plant Species that Experience Positive and Negative Plant–Soil Feedback. When we refer to a species as a positive or a negative-feedback species, we refer to its conspecific plant–soil feedback.

exactly drives such observed increases 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 [15,16]. Many of these plant enemies, such as pathogenic fungi, are specialized on

[8]Helmholtz Centre for Environmental Research, Physiological Diversity – UFZ, Leipzig, Germany
[9]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany
[10]Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China
[11]Institute of Biology, Section Plant Ecology and Phytochemistry, Leiden University, 2300, RA, Leiden, The Netherlands

*Correspondence:
madhav.thakur@iee.unibe.ch
(M.P. Thakur).

Box 2. 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, and 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 one species) to polycultures (mixtures), containing two to usually ~20 species (occasionally more). Species compositions are randomly selected from a larger pool of co-occurring species 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 [97]. A few BEF experiments used a removal approach, where plant species are manually removed from communities to simulate extinctions [42,98]. The early BEF experiments were all done in grasslands, but an increasing number of experiments have also been established in forests [99]. Recently, there has been 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 nonrandom and correlated with diversity. Therefore, such studies aim to determine the importance of diversity changes alongside these other factors [80].

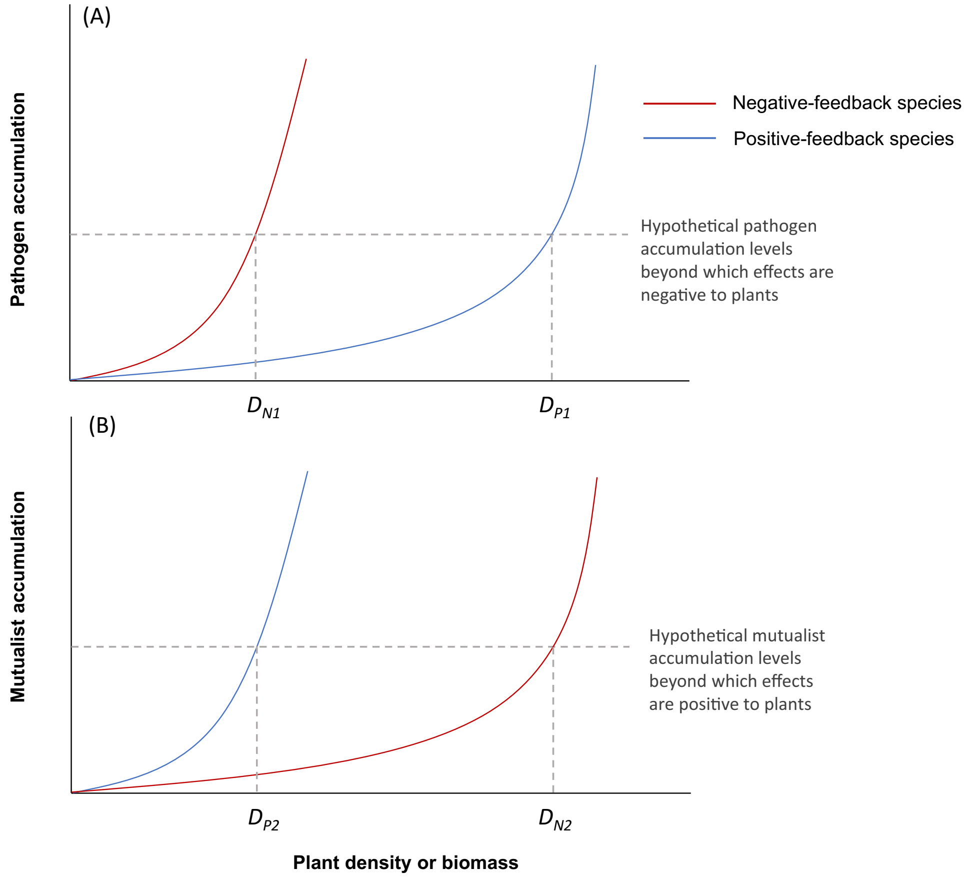
particular host plants and become increasingly abundant in their host plant monocultures [17,18]. Therefore, accumulation of these antagonists over time in monocultures could cause a progressive decline in monoculture biomass relative to the biomass of diverse plant communities [15,19].

BEF researchers have repeatedly called for investigations into the processes that operate in diverse plant communities to enhance their performance relative to monocultures [20,21]. 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 [21]. However, we know little 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 [10,14,15,21]. Among several biotic feedbacks that can be identified in species-rich plant communities [21], we focus here on temporal shifts in PSF in species-rich plant communities (Box 1).

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 [22,23] (see Figure I in Box 1). The progressive decline in productivity in certain plant monocultures could 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 because both conspecific and heterospecific PSFs simultaneously occur in diverse plant communities [23,24]. Heterospecific feedbacks are particularly difficult to predict because 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 1) [25]. However, studies have shown that grasses and forbs generally grow better in soils previously conditioned by species from a different functional group [23,26,27]. Moreover, closely related plant species (i.e., species having a low phylogenetic distance) exert greater negative heterospecific feedback compared with distantly related plants, mainly because the likelihood of soil pathogens infecting other plants is higher when the plants are phylogenetically related to the host plant [5,28,29]. Thus, the factors that can predict the magnitude and direction of conspecific and heterospecific feedbacks in diverse plant communities are essential ingredients for incorporating PSF knowledge into BEF research.

Building upon advances in how PSF may operate in diverse plant communities [24,30], and how PSF can be predicted in the field [26,31], we highlight three processes that occur in species-rich plant communities that can help us to understand the temporal dynamics of diversity–productivity



Trends in Ecology & Evolution

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 (A)], whereas a positive-feedback species benefits from mutualist effects at low densities [D_{P2} in (B)]. By contrast, a negative feedback species needs to reach a higher density to benefit from mutualists [D_{N2} in (B)], whereas positive-feedback species suffer from pathogens at high densities [D_{P1} in (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) depending on density dependence in pathogens and mutualists, and also on the density or biomass of host plants.

relationships (Figure 2): (i) spatial plant redistribution and local changes in plant abundance; (ii) phenotypic shifts in plant traits; and (iii) 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 2).

Spatial Redistribution and Shifts in Abundance

Several grassland plants overcome conspecific negative feedbacks by shifting their local spatial distribution, such that they occupy different soil patches over time [32,33]. Such a response usually reduces the accumulation of specialized soil-borne pathogens on a given host plant at a given location [34,35]. In monoculture plots, the spatial redistribution of plant individuals is

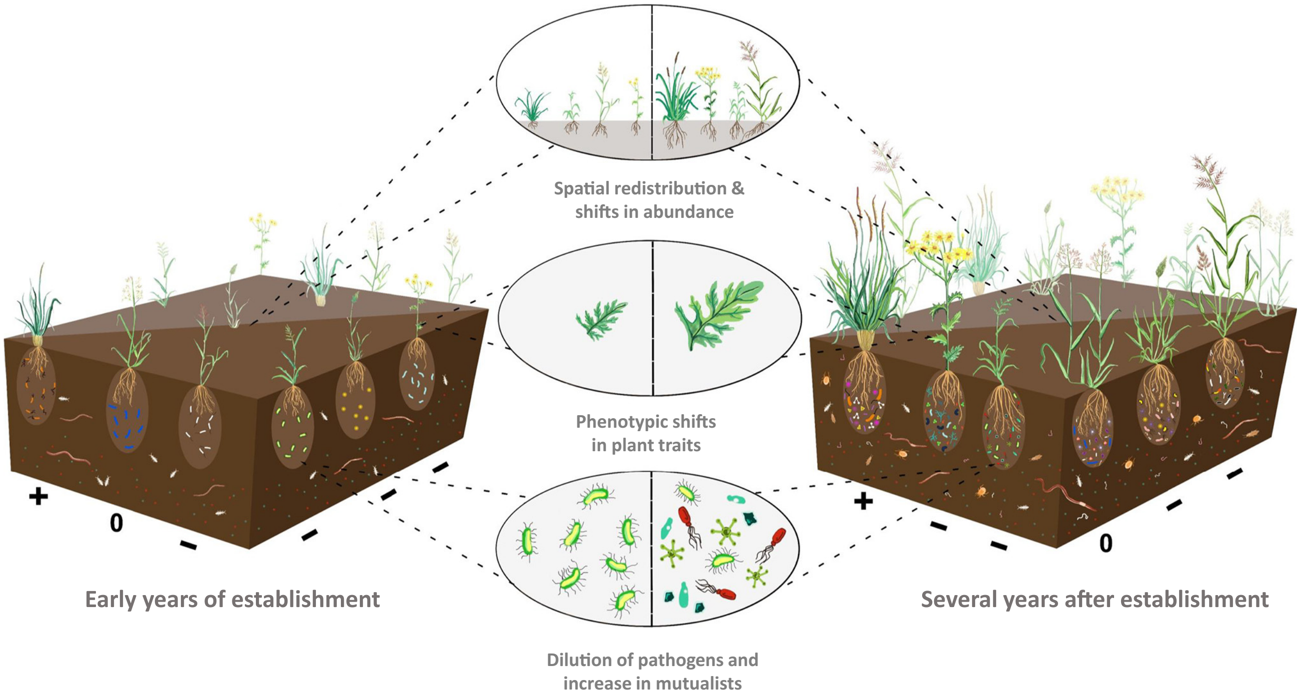


Figure 2. Plant–Soil Feedback (PSF) Will Change over Time in Diverse Plant Communities. After several years, PSF in diverse plant communities changes mainly via three nonmutually exclusive temporal processes: spatial redistribution and changes in plant abundance (mainly of negative feedback species); phenotypic shifts in plant traits (e.g., resource acquisition traits, such as 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 –. Spatial redistribution is shown via spatial rearrangement of plant species. Changes in abundance are 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.

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 (see Figure I in Box 1) than for species with neutral or positive feedbacks (Figure 1) [36]. This prediction could be tested with data from biodiversity experiments where the spatial distribution (or turnover) of species is recorded over time, such as in permanent quadrats in each plot.

In a diverse plant community, individuals of plant species experiencing negative conspecific feedback 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 [22,31,37,38]. 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 [39–41]. However, within a high diversity plot, the extent of heterospecific feedback that arises by spatial shuffling will likely vary depending on the functional difference (traits and/or groups) and phylogenetic distance of the neighbors 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 that are functionally and phylogenetically diverse.

The temporal diversity–productivity relationship is often argued to depend on environmental fluctuations over time [42,43]. Although these fluctuations are assumed to be largely driven by exogenous environmental conditions [43], the biotic interactions between neighboring 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 exert different PSF on component plants compared with soils where spatial redistribution is lower. These patch-specific differences in PSF can be linked to variation in the temporal (a)synchrony of plants in species-rich communities. Furthermore, 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 [38]. It will also be important to examine the relationships 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 relationships.

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 [44]. This is particularly true for traits related to (interspecific) competition, such as specific leaf area and plant height, which are crucial for resource acquisition [44]. We can expect that selection for competition-related traits in mixed plant communities can enhance trait divergence, thereby improving the complementary use of limited resources [44,45]. We propose that shifts in competition-related traits in a plant also affect the strength of PSF because plant traits are often associated with how they affect the soil biotic and abiotic environments [46]. That is, if a species with negative feedback exhibits greater divergence in its competition-related traits from its neighboring species, we could also expect divergence in how the two species will influence their local soil environment and, thus, their effects on both conspecific and heterospecific plants. For instance, root traits affecting plant competition for soil resources, such as specific root length [47,48], can alter the strength of PSF [49]. 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 [44] (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 to variation in plant defense traits in monocultures [50]. Indeed, selection for traits related to defense 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 [44,50]. Given the role of root traits in acquiring limited resources [51], divergent selection in root traits over time in diverse plant communities can occur, contributing to niche differentiation for resource acquisition. However, whether temporal shifts in the strength of PSF due to spatial redistribution (and changes in plant abundance) could affect the selective environment for above- and belowground plant traits remains relatively unexplored. This line of inquiry is important because the biotic neighborhood is a crucial determinant of phenotypic plasticity in plants [52].

Trait evolution in diverse plant communities is limited not only to competition and defense-related traits, but also to life-history traits. A recent study showed that the longevity of a plant species growing in a diverse plant community increased, while its reproduction was delayed [53]. Examining the effects of trait evolution on PSF in long-running plant diversity experiments can unravel how evolutionary processes can explain temporal diversity–productivity relationships. Currently, there is growing interest in applying the principles of eco-evolutionary feedbacks to both BEF and PSF research [54,55]. In line with these trends, our current understanding of character displacement in competition-related traits in long-running biodiversity experiments can be extended to other traits and could provide an important basis for investigating how divergent selection for niche differentiation both drives, and is driven by, PSF. Conversely, if trait evolution in plants promotes positive PSF for certain plant species, productivity in diverse plant communities can still increase due to the presence of high biomass plant species [56] (also referred as positive selection effect [57]). We suggest that a better understanding of PSF in relation to both competition- and defense-related plant traits above- and belowground in diverse plant communities is a key step to obtaining a mechanistic understanding of temporal diversity–productivity relationships [58,59].

Dilution of Soil Pathogens and Increase in Soil Mutualists

Epidemiological studies have long shown that diversity slows the spread of diseases due to greater dilution of pathogens [60,61]. A dilution of pathogens essentially means that their net effect on potential hosts decreases. This occurs through several mechanisms, including effects of other species on trophic regulation of the pathogens by their predators, reduced transmission, or a decrease in host quality [62,63]. Therefore, pathogen dilution would result in a reduction of negative PSF. The dilution of soil fungal pathogens was recently demonstrated in a plant-diversity experiment, where >50% of pathogenic fungal operational taxonomic units (OTUs) found in monocultures were absent from diverse plant communities comprising the same plant species [17]. The exact mechanism by which pathogen dilution occurs in diverse plant communities, 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 multiplant environment [15,64]. Trophic control of fungal or other plant pathogens in the soil is another mechanism underlying pathogen dilution, because diverse plant communities can sustain a greater density and diversity of microbial predators compared with plant monocultures [30,65,66].

Soil-microbial diversity and biomass increase in plots with a high diversity of plants in field experiments [67,68]. 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 or mycorrhizal fungi) over pathogenic microorganisms [19], this would further reduce the strength of negative feedback experienced by plants [69]. 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. Therefore, we might 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 nonsown plants is allowed, saturation might be less likely because newly colonizing plant species would continue to perturb the pathogen dynamics [70,71].

PSF can also vary due to plant mutualists in the soil that benefit plants by acquiring nutrients or suppressing pathogens [72,73] (Figure 1). For instance, a greater diversity of mutualistic soil microorganisms decreases the strength of negative PSF [69,74]. 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 [19]. 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 [50,75]. If such soil microbe-driven plant-trait variation reduces negative PSF, 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 (see Figure I in Box 1). Such positive mutualist effects can also negatively influence species diversity in species-rich communities because greater mutualist accumulation can promote the dominance of a few selective plants [76]. 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 the trophic regulation of soil pathogen and mutualist may further affect pathogen dilution and/or mutualist accumulation [77]. Indeed, the temporal shifts in PSF will eventually depend on how the relationship between the plant and its pathogens, and mutualists changes over time, because 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

To integrate PSF and BEF research, a key question that needs further attention is how the three temporal processes we discussed operate in real-world ecosystems (Box 2) [78]. The heterogeneous colonization patterns of plants in real-world ecosystems makes them temporally more dynamic (i.e., there is greater spatiotemporal turnover of plant species, including changes in species richness) in these systems than in many long-running BEF experiments [79]. Real-world ecosystem studies have shown that greater plant diversity also leads to increased plant-biomass production among other ecosystem functions [79,80]. In real-world ecosystems, plant identity will likely have 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 [5,81,82]. 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, 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 such as 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 PSF, given that the temporal strengthening of diversity–productivity relationship has also been shown in forest ecosystems [14].

The three processes discussed here (Figure 2) are not exhaustive, because 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, thereby increasing or decreasing the strength of PSF. For instance, there is increasing evidence that aboveground herbivory by insects and mammals affects the functioning of soil microbial communities [83,84] and, therefore, potentially the magnitude and direction of PSF. For instance, functional shifts in soil microbial communities could affect the temporal build-up of the dilution effect in diverse plant communities. Aboveground herbivores can further reduce investment by the plant in competition-related traits over defense- and/or tolerance-related traits [85,86], thereby affecting trait evolution and PSF relationships [87]. Herbivory can also shift the competitive (a)symmetry among neighboring plants, and this, in turn, can have consequences for the temporal shifts in PSF [88–90], 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 influences the performance of plants in diverse plant communities. These disturbances can alter the proposed three processes by either reducing plant diversity or 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 [91–93], 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 the 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, thereby strengthening the diversity–productivity relationship over time and causing PSF, particularly for negative feedback species, to vary from year to year, which might promote temporal niche partitioning in diverse plant communities [94,95]. We further advocate for the combination of ecological (e.g., spatial processes) and evolutionary (e.g., trait evolution) approaches to help integration of 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).

Outstanding Questions

How does spatial redistribution of plants in diverse plant communities affect pathogen dilution and mutualist accumulation over time?

What are the relationships between the evolution of competition-related traits and pathogen dilution in diverse plant communities?

What are the roles of environmental variations in determining spatial and temporal partitioning of PSF in diverse plant communities?

Do plants from diverse plant communities experience negative, neutral ,or positive feedback as communities age?

How does PSF contribute to temporal variations in plant–diversity effects on plant biomass in real-world ecosystems?

Can plants evolve to change PSF over time in diverse plant communities?

How will aboveground plant enemies (e.g., herbivores and pathogens) affect spatial redistribution, shifts in competition-related traits, and pathogen dilution (and mutualist accumulation) in diverse plant communities?

How will stochastic disturbances (e.g., induced by anthropogenic climate change) affect the temporal variation in plant diversity effects on plant-biomass production, and how is PSF related to such effects?

Acknowledgments

We thank three anonymous reviewers and Andrea Stephens for constructive suggestions that substantially improved the manuscript. We thank Pryianka Ambhavane (https://ambypriya.myportfolio.com/) for her help in drawing figures.

Author Contributions

M.P.T. and T.M.B. conceived the main idea and wrote the manuscript. All authors contributed substantially to further develop the main idea and to revise the manuscript.

Declaration of Interests

No interests are declared.

References

1. van der Putten, W.H. *et al.* (2013) Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276
2. Bennett, J.A. and Klironomos, J. (2019) Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. *New Phytol.* 222, 91–96
3. Maron, J.L. *et al.* (2016) Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology* 97, 2055–2063
4. Eppinga, M.B. *et al.* (2018) Frequency-dependent feedback constrains plant community coexistence. *Nat. Ecol. Evol.* 2, 1403–1407
5. Crawford, K.M. *et al.* (2019) When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecol. Lett.* 22, 1274–1284
6. Tilman, D. *et al.* (2014) Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Syst.* 45, 471–493
7. Loreau, M. *et al.* (2001) Ecology: biodiversity and ecosystem functioning: current knowledge and future challenges. *Science (80-.)* 294, 804–808
8. Reich, P.B. *et al.* (2012) Impacts of biodiversity loss escalate through time as redundancy fades. *Science (80-.)* 336, 589–592
9. Cardinale, B.J. *et al.* (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci. U. S. A.* 104, 18123–18128
10. Vogel, A. *et al.* (2019) A new experimental approach to test why biodiversity effects strengthen as ecosystems age. *Adv. Ecol. Res.* 61, 221–264
11. Meyer, S.T. *et al.* (2016) Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity. *Ecosphere* 7, e01619
12. Ravenek, J.M. *et al.* (2014) Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. *Oikos* 123, 1528–1536
13. Van Ruijven, J. and Berendse, F. (2005) Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. U. S. A.* 102, 695–700
14. Guerrero-Ramírez, N.R. *et al.* (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* 1, 1639–1642
15. van Ruijven, J. *et al.* (2020) Do soil-borne fungal pathogens mediate plant diversity–productivity relationships? Evidence and future opportunities. *J. Ecol.* 108, 1810–1821
16. Dietrich, P. *et al.* (2020) Nematode communities, plant nutrient economy, and life-cycle characteristics jointly determine plant monoculture performance over 12-years. *Oikos* 129, 466–479
17. Mommer, L. *et al.* (2018) Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. *New Phytol.* 218, 542–553
18. Maron, J.L. *et al.* (2011) Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecol. Lett.* 14, 36–41
19. Eisenhauer, N. *et al.* (2012) Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic Appl. Ecol.* 13, 571–578
20. Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474
21. Barry, K.E. *et al.* (2019) The future of complementarity: disentangling causes from consequences. *Trends Ecol. Evol.* 34, 167–180
22. Kulmatiski, A. *et al.* (2008) Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.* 11, 980–992
23. Cortois, R. *et al.* (2016) Plant–soil feedbacks: role of plant functional group and plant traits. *J. Ecol.* 104, 1608–1617
24. Kulmatiski, A. *et al.* (2012) Plant-soil feedbacks provide an additional explanation for diversity-productivity relationships. *Proc. R. Soc. B Biol. Sci.* 279, 3020–3026
25. Bezemer, T.M. *et al.* (2006) Plant species and functional group effects on abiotic and microbial soil properties and plant-soil feedback responses in two grasslands. *J. Ecol.* 94, 893–904
26. Heinen, R. *et al.* (2020) Plant community composition steers grassland vegetation via soil legacy effects. *Ecol. Lett.* 23, 973–982
27. Petermann, J.S. *et al.* (2008) Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89, 2399–2406
28. Wandrag, E.M. *et al.* (2020) Phylogenetic signals and predictability in plant–soil feedbacks. *New Phytol.* 228, 1440–1449
29. Kempel, A. *et al.* (2018) Plant soil feedback strength in relation to large-scale plant rarity and phylogenetic relatedness. *Ecology* 99, 597–606
30. Guerrero-Ramírez, N.R. *et al.* (2019) Diversity-dependent plant–soil feedbacks underlie long-term plant diversity effects on primary productivity. *Ecosphere* 10, e02704
31. Chung, Y.A. *et al.* (2019) Connecting plant–soil feedbacks to long-term stability in a desert grassland. *Ecology* 100, e02756
32. Olff, H. *et al.* (2000) Small-scale shifting mosaics of two dominant grassland species: The possible role of soil-borne pathogens. *Oecologia* 125, 45–54
33. Vincenot, C.E. *et al.* (2017) Plant–soil negative feedback explains vegetation dynamics and patterns at multiple scales. *Oikos* 126, 1319–1328
34. Real, L.A. and McElhany, P. (1996) Spatial pattern and process in plant-pathogen interactions. *Ecology* 77, 1011–1025
35. Gilbert, G.S. (2002) Evolutionary ecology of plant diseases in natural ecosystems. *Annu. Rev. Phytopathol.* 40, 13–43
36. Bonanomi, G. *et al.* (2005) Negative plant-soil feedback and species coexistence. *Oikos* 111, 311–321
37. Bezemer, T.M. *et al.* (2018) Plant competition alters the temporal dynamics of plant-soil feedbacks. *J. Ecol.* 106, 2287–2300
38. in't Zandt, D. *et al.* (2021) Species abundance fluctuations over 31 years are associated with plant-soil feedback in a species-rich mountain meadow. *J. Ecol.* 109, 1511–1523
39. Hendriks, M. *et al.* (2015) Spatial heterogeneity of plant-soil feedback affects root interactions and interspecific competition. *New Phytol.* 207, 830–840
40. Xue, W. *et al.* (2018) Spatial heterogeneity in plant–soil feedbacks alters competitive interactions between two grassland plant species. *Funct. Ecol.* 32, 2085–2094
41. Wubs, E.R.J. and Bezemer, T.M. (2018) Plant community evenness responds to spatial plant–soil feedback heterogeneity primarily through the diversity of soil conditioning. *Funct. Ecol.* 32, 509–521
42. Kardol, P. *et al.* (2018) Long-term effects of species loss on community properties across contrasting ecosystems. *Nature* 557, 710–713
43. Loreau, M. and de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115
44. Zuppinger-Dingley, D. *et al.* (2014) Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515, 108–111
45. Turcotte, M.M. and Levine, J.M. (2016) Phenotypic plasticity and species coexistence. *Trends Ecol. Evol.* 31, 803–813
46. Baxendale, C. *et al.* (2014) Are plant-soil feedback responses explained by plant traits? *New Phytol.* 204, 408–423
47. Mommer, L. *et al.* (2011) Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. *Plant Soil* 344, 347–360
48. Fort, F. *et al.* (2014) Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. *Funct. Ecol.* 28, 1030–1040
49. Wilschut, R.A. *et al.* (2019) Root traits and belowground herbivores relate to plant–soil feedback variation among congeners. *Nat. Commun.* 10, 1564
50. Hahl, T. *et al.* (2020) Plant responses to diversity-driven selection and associated rhizosphere microbial communities. *Funct. Ecol.* 34, 707–722
51. Mueller, K.E. *et al.* (2013) Root depth distribution in a long-term grassland experiment. *Ecology* 94, 787–793
52. Abakumova, M. *et al.* (2016) Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytol.* 211, 455–463

53. Roeder, A. *et al.* (2019) Increasing plant diversity of experimental grasslands alters the age and growth of Plantago lanceolata from younger and faster to older and slower. *Oikos* 128, 1182–1193
54. terHorst, C.P. and Zee, P.C. (2016) Eco-evolutionary dynamics in plant–soil feedbacks. *Funct. Ecol.* 30, 1062–1072
55. Eisenhauer, N. *et al.* (2019) Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. *Res. Ideas Outcomes Open Sci. J.* 5, e47042
56. Jing, J. *et al.* (2015) Complementarity and selection effects in early and mid-successional plant communities are differentially affected by plant-soil feedback. *J. Ecol.* 103, 641–647
57. Loreau, M. and Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76
58. Schroeder, J.W. *et al.* (2020) Mutualist and pathogen traits interact to affect plant community structure in a spatially explicit model. *Nat. Commun.* 11, 2204
59. Lau, J.A. and Lennon, J.T. (2011) Evolutionary ecology of plant-microbe interactions: Soil microbial structure alters selection on plant traits. *New Phytol.* 192, 215–224
60. Civitello, D.J. *et al.* (2015) Biodiversity inhibits parasites: Broad evidence for the dilution effect. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8667–8671
61. Keesing, F. *et al.* (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468, 647–652
62. Ostfeld, R.S. and Keesing, F. (2012) Effects of host diversity on infectious disease. *Annu. Rev. Ecol. Evol. Syst.* 43, 157–182
63. Johnson, P.T.J. and Thieltges, D.W. (2010) Diversity, decoys and the dilution effect: How ecological communities affect disease risk. *J. Exp. Biol.* 213, 961–970
64. Wilschut, R.A. and Geisen, S. (2021) Nematodes as drivers of plant performance in natural systems. *Trends Plant Sci.* 26, 237–247
65. Eisenhauer, N. *et al.* (2011) Changes in plant species richness induce functional shifts in soil nematode communities in experimental grassland. *PLoS ONE* 6, e24087
66. Latz, E. *et al.* (2012) Plant diversity improves protection against soil-borne pathogens by fostering antagonistic bacterial communities. *J. Ecol.* 100, 597–604
67. Thakur, M.P. *et al.* (2015) Plant diversity drives soil microbial biomass carbon in grasslands irrespective of global environmental change factors. *Glob. Chang. Biol.* 21, 4076–4085
68. Prober, S.M. *et al.* (2015) Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecol. Lett.* 18, 85–95
69. Semchenko, M. *et al.* (2018) Fungal diversity regulates plant-soil feedbacks in temperate grassland. *Sci. Adv.* 4, eaau4578
70. Trognitz, F. *et al.* (2016) The role of plant-microbiome interactions in weed establishment and control. *FEMS Microbiol. Ecol.* 92, 1–15
71. Telfer, S. and Bown, K. (2012) The effects of invasion on parasite dynamics and communities. *Funct. Ecol.* 26, 1288–1299
72. van der Putten, W.H. *et al.* (2016) Where, when and how plant–soil feedback matters in a changing world. *Funct. Ecol.* 30, 1109–1121
73. Revillini, D. *et al.* (2016) The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Funct. Ecol.* 30, 1086–1098
74. Bever, J.D. *et al.* (2013) Microbial phylotype composition and diversity predicts plant productivity and plant-soil feedbacks. *Ecol. Lett.* 16, 167–174
75. Dietrich, P. *et al.* (2020) Diverse plant mixtures sustain a greater arbuscular mycorrhizal fungi spore viability than monocultures after 12 years. *J. Plant Ecol.* 13, 478–488
76. Zahra, S. *et al.* (2021) Do reverse Janzen-Connell effects reduce species diversity? *Trends Ecol. Evol.* 36, 387–390
77. Thakur, M.P. and Geisen, S. (2019) Trophic regulations of the soil microbiome. *Trends Microbiol.* 27, 771–780
78. Manning, P. *et al.* (2019) Transferring biodiversity-ecosystem function research to the management of ‘real-world’ ecosystems. *Adv. Ecol. Res.* 61, 323–356
79. Jochum, M. *et al.* (2020) The results of biodiversity–ecosystem functioning experiments are realistic. *Nat. Ecol. Evol.* 4, 1485–1494
80. van der Plas, F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.* 94, 1220–1245
81. Verbeek, J.D. and Kotanen, P.M. (2019) Soil-mediated impacts of an invasive thistle inhibit the recruitment of certain native plants. *Oecologia* 190, 619–628
82. Zhang, Z. and van Kleunen, M. (2019) Common alien plants are more competitive than rare natives but not than common natives. *Ecol. Lett.* 22, 1378–1386
83. Andriuzzi, W.S. and Wall, D.H. (2017) Responses of belowground communities to large aboveground herbivores: meta-analysis reveals biome-dependent patterns and critical research gaps. *Glob. Chang. Biol.* 23, 3857–3868
84. Bardgett, R.D. *et al.* (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biol. Biochem.* 30, 1867–1878
85. Ballhorn, D.J. *et al.* (2014) Chemical defense lowers plant competitiveness. *Oecologia* 176, 811–824
86. Strauss, S.Y. and Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* 14, 179–185
87. Heinze, J. *et al.* (2020) Plant–soil feedback effects altered by aboveground herbivory explain plant species abundance in the landscape. *Ecology* 101, e03023
88. Borgström, P. *et al.* (2016) Aboveground insect herbivory increases plant competitive asymmetry, while belowground herbivory mitigates the effect. *PeerJ* 2016, e1867
89. Backmann, P. *et al.* (2019) Delayed chemical defense: timely expulsion of herbivores can reduce competition with neighboring plants. *Am. Nat.* 193, 125–139
90. Olff, H. and Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13, 261–265
91. Wagg, C. *et al.* (2017) Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. *Ecology* 98, 2952–2961
92. Isbell, F. *et al.* (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577
93. van Moorsel, S.J. *et al.* (2020) Co-occurrence history increases ecosystem stability and resilience in experimental plant communities. *Ecology* 102, e03205
94. Tredennick, A.T. *et al.* (2017) The relationship between species richness and ecosystem variability is shaped by the mechanism of coexistence. *Ecol. Lett.* 20, 958–968
95. Chesson, P. (2000) General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.* 58, 211–237
96. Miller, E.C. *et al.* (2019) Plant-driven changes in soil microbial communities influence seed germination through negative feedbacks. *Ecol. Evol.* 9, 9298–9311
97. Weisser, W.W. *et al.* (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. *Basic Appl. Ecol.* 23, 1–73
98. Díaz, S. *et al.* (2003) Functional diversity revealed by removal experiments. *Trends Ecol. Evol.* 18, 140–146
99. Verheyen, K. *et al.* (2016) Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* 45, 29–41