Trends in
Ecology & Evolution

CellPress

Review

Plant litter strengthens positive biodiversity–ecosystem functioning relationships over time

Wei-Ping Zhang,[1] Dario Fornara,[2] Hao Yang,[1] Rui-Peng Yu,[1] Ragan M. Callaway,[3] and Long Li [1,*]

Plant biodiversity–productivity relationships become stronger over time in grasslands, forests, and agroecosystems. Plant shoot and root litter is important in mediating these positive relationships, yet the functional role of plant litter remains overlooked in long-term experiments. We propose that plant litter strengthens biodiversity–ecosystem functioning relationships over time in four ways by providing decomposing detritus that releases nitrogen (N) over time for uptake by existing and succeeding plants, enhancing overall soil fertility, changing soil community composition, and reducing the impact of residue-borne pathogens and pests. We bring new insights into how diversity–productivity relationships may change over time and suggest that the diversification of crop residue retention through increased residue diversity from plant mixtures will improve the sustainability of food production systems.

Highlights

Nitrogen (N) inputs from legume residues over the long-term contribute to improve soil N cycling and the productivity of succeeding plants in species-diverse ecosystems.

Litter mixtures enhance soil fertility, thus enhancing biomass production, which in turn creates positive diversity–productivity feedback in the long-term.

Positive effects of litter diversity on the composition and diversity of soil organisms increase over time.

Residue-borne pathogens and pests gradually accumulate through litter input from monocultures, whereas diverse plant-litter mixtures reduce the incidence and spread of residue-borne pathogens and pests in the long-term.

Plant litter can strengthen biodiversity–ecosystem functioning relationships in both natural and managed ecosystems.

Appropriate management of residues from plant mixtures across multiple growing seasons can promote the sustainability of food production systems.

Biodiversity effects on productivity increase over time

Positive plant diversity–productivity relationships become stronger over time in grasslands [1], forests [2–4], and agroecosystems [5,6]. A meta-analysis of 44 biodiversity experiments showed that species mixtures produced an average of 1.7 times more biomass compared with species monocultures; moreover, the impacts of plant diversity on biomass production became significantly stronger over the duration of the experiments [7]. One such example comes from two long-term (≥13 years) grassland experiments established in Minnesota, USA. Here, in statistical terms, the exponent from the power function of the relative yield (i.e., dividing plot-level values by the mean monoculture yield) of total biomass in relation to species richness increased from 0 toward 1 over time in both experiments. This indicated that the effects of species diversity on plant biomass increased and became less saturating over time [1]. Similarly, in subtropical forests, the net biodiversity effect on stand volume increased through time for mixtures of all species-richness levels [2,3]. Urgoiti *et al.* [4] found that the positive effects of tree species diversity on temperate forest productivity were only observed after 9 years. In agroecosystems, the yield advantages of **intercropping** (see Glossary) maize (*Zea mays* L.)/soybean (*Glycine max* L.) and maize/peanut (*Arachis hypogaea* L.) increased over time, but only in the absence of N fertilization [5]. Identifying why the effects of plant diversity strengthen over time helps us to understand the fundamental mechanisms of how biodiversity drives ecosystem function in general.

The mechanisms thought to underlie the development of stronger biodiversity effects on ecosystem function over time mainly involve the role of living plants and their interactions with the soil environment. These might drive increases in the functioning of high-diversity communities or decreases in the functioning of low-diversity communities, or both [8]. Mechanistically, the effects of **complementarity** in resource acquisition and use, as well as positive ecosystem feedbacks

[1]Beijing Key Laboratory of Biodiversity and Organic Farming, Key Laboratory of Plant and Soil Interactions, Ministry of Education, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China
[2]Davines Group-Rodale Institute European Regenerative Organic Center (EROC), Via Don Angelo Calzolari 55/a, 43126, Parma, Italy

on soil N cycling, tend to accumulate over time in high-diversity communities [1]. Concurrently, the accumulation of natural enemies and the high pressure from species-specific pathogens limit productivity in low-diverse communities [9]. Thus, strengthened biodiversity effects could result from lower pathogen accumulation over time (compared with monocultures) or from increasingly complementary resource use and nutrient accumulation in **plant mixtures** [1,9,10]. In addition, long-term intercropping can enhance **soil fertility** via increases in soil organic matter, total N, and soil macroaggregates compared with monocultures, all of which contribute to increasing yield advantages in intercropping over time [6].

[3]Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA

*Correspondence:
lilong@cau.edu.cn (L. Li).

Regardless of the mechanism involved, the remarkably consistent increase in positive diversity–ecosystem functioning over time indicates that the cumulative transformation of the biotic and abiotic environment by vegetation is a key process by which biodiversity regulates ecosystem function. One of the primary ways that plants transform their environments is through the long-term accumulation of **plant litter**. Plant litter (or **crop residues**), which originate from living plants (temporal link), remain in close contact with the soil (spatial link) for long periods [11] and, thus, can have a significant role in mediating plant–soil interactions in the long-term. Terrestrial ecosystems produce a large amount of plant litter, and litter effects on ecosystem functioning are generally well known. Approximately half the organic carbon (C) produced by terrestrial plants contributes to the global plant-litter residue pool [12]. Globally, an estimated 3758 × 10^6 Mg of residue is produced annually by 27 main food crops [13]. The decomposition of litter can profoundly influence key ecological processes, such as the formation of soil organic matter [14], nutrient cycling [15], energy flow, and plant growth [16,17]. In addition, litter decomposition may directly or indirectly influence plant–plant interactions [18], community succession [19], the diversity and activity of microorganisms [17,20], and **biodiversity–ecosystem function (BEF)** relationships [21]. For example, litter decomposition is closely linked to **direct** (e.g., nutrient enrichment) and **indirect** (e.g., altered **soil biodiversity**) **facilitation**, which can contribute to positive BEF relationships [22]. Greater plant species diversity significantly affects the quantity, quality, and chemical diversity of plant litter [23,24]. After plants die, their diversity still has substantial effects on ecosystem functioning (i.e., litter decomposition) in forests, grasslands, and wetlands [25]. Plant diversity increases productivity and further enhances aboveground litterfall and root litter inputs to soils [26,27]. Changes in the quantity and quality of litter mixtures can greatly influence decomposition processes, thus potentially altering ecosystem functioning [25,28]; however, the potential roles of plant litter in mediating positive diversity–productivity relationships in the long-term remain poorly understood.

The role of plant litter in strengthening the plant diversity–productivity relationship over time

We suggest that diversity-induced changes in plant litter further enhance and strengthen positive biodiversity effects on ecosystem functioning over time in four different ways (Figure 1).

Decomposition of plant litter contributes to N uptake of succeeding plants

N fixation by legumes and N transfer to nonlegumes contribute to overyielding and higher N use efficiency in species mixtures [5,29], a process most closely linked mechanistically to facilitation [22]. Using ^{15}N natural abundance-based techniques, an estimated 30–83% of nonlegume N is derived from legume-fixed N, thus representing up to 30–40 kg N ha^{-1} [29]. Belowground N transfer from legumes to nonlegumes can occur through three pathways (Figure 1, arrow a; Figure 2): (i) exudation of soluble N compounds from legumes and direct uptake by nonlegumes [30]; (ii) direct transfer of N mediated by plant-associated mycorrhizal fungi [31]; and (iii) decomposition of legume root tissues and nodules and subsequent uptake of mineralized N by neighboring plants [32]. N transfer through the senescence and decomposition of roots and nodules is generally a slower process than N transfer via root exudates or mycorrhizal fungal networks, and the former mostly contributes to N uptake during the later stages of plant growth within a growing season or in subsequent growing seasons [33]. Previous studies of N transfer focused on either species mixtures within a growing season or rotations across growing seasons. The contribution of legumes to BEF relationships is well recognized in both short- and long-term biodiversity experiments [1,10,34]. However, long-term N effects including, for example, the contribution of legume residues to the N uptake of succeeding nonlegumes have received less attention.

Belowground N transfer from legume residues to succeeding plants can contribute to enhance the diversity effect over time (Figure 2). Legume root and nodule decomposition contribute large amounts of N to **cover crop** and **crop rotation** systems and to legume–grass forage mixtures [32,35]. Roots of legume-based cover crops can represent 31–50% of total plant N (153–226 kg N ha^{-1}), which can contribute to the yield of succeeding crops [36]. The main pathway of belowground N transfer from the legume *Stylosanthes guianensis* to the associated grass *Brachiaria decumbens* was via decaying roots rather than via root exudates or mycorrhizal fungal networks between the legume and the grass [37]. In a 2-year field intercropping experiment, the maize partial land equivalent ratio (PLER) of maize/soybean and maize/peanut intercropping systems not receiving N fertilization increased and resulted in higher total LERs of intercropping systems during the second year of cultivation [5]. Moreover, the number of ears per unit area or grains per ear of maize was very low in monocultures without N fertilization, but remained relatively high in intercropping during the second year of the experiment. The decomposition of legume roots and nodules in the long-term can contribute to N uptake of succeeding maize plants [33], possibly explaining the overyielding of intercropping over time without N fertilization [5].

Several meta-analyses and long-term experimental studies have shown how the mechanisms underlying the increasingly positive effect of diversity on biomass productivity shifted from **selection** to complementarity effects as the experiments progressed [1,2,7,38]. The decomposition of shoot and root litter (including legumes and nonlegumes) can provide extra N to plants in the succeeding year [36]. This extra N supply, together with complementary N use in time and space, and N transfer within a growing season in species mixtures [1,5,7,38] could help explain the stronger biodiversity effect on productivity over time (Figure 2). In addition to root litter, aboveground litter may also be an important source for N transfer. For example, two-thirds of biologically fixed N transferred from *Faidherbia* trees (*Faidherbia albida*; Fabaceae) into the leaves of surrounding maize plants was attributed to N release from the decomposition of tree leaf litter [31]. The decomposition of nonleguminous litter is also an important N source in unfertilized ecosystems. A positive relationship between plant species richness and productivity emerged during the second year and strengthened with time in a 4-year biodiversity experiment without legumes [38], possibly because of increased N input due to litter decomposition and increased nutrient use efficiency under high species richness conditions [1,7,34,38].

In addition to N, the transfer of phosphorous (P), potassium (K), and other elements from remaining litter residues is an important potential source of nutrients for subsequent crops. The percentage of P contained in wheat-derived residue ranged from 9% to 44% in a dual-labeling experiment [39]. Moreover, the addition of root residues from a mixture of maize and faba bean (*Vicia faba* L.) enhanced intercropping advantages in terms of total P content in a P-deficient soil [40].

Changes in the quantity and quality of litter mixtures enhance soil fertility

Higher plant diversity increases plant biomass production, which, in turn, can contribute to other properties of soil fertility (besides N mentioned previously) as shoot and root biomass are returned

Glossary

Biodiversity-ecosystem function (BEF): effect of species, genetic, and functional diversity on ecosystem functioning.
Biofumigation: use of plant material and naturally produced compounds to control pests.
Complementarity effect: more efficient use of available resources deriving from interspecific facilitation and/or niche partitioning in species mixtures.
Continuous cropping obstacle: abnormal growth and development of crops caused by the continuous cultivation of the same crop species or its relatives in the same field.
Cover crop: any living ground cover that is planted with or after a main crop to protect the soil from erosion; it is usually killed before the next crop is planted.
Crop diversification: intentional addition of functional biodiversity to cropping systems at multiple spatial (e.g., crop mixture, intercropping, and cover crops) and/or temporal scales (e.g., crop rotation).
Crop mixture: two or more different crop species or varieties are grown simultaneously on the same field in alternative rows or mixture with no distinct row pattern.
Crop residues: decaying parts of the crop plant that are not harvested.
Crop rotation: agricultural practice of growing a series of different crop species in the same field across multiple growing seasons.
Direct facilitation: one plant benefits neighboring plants by habitat amelioration or resource enrichment.
Facilitation: direct and indirect positive effects of plants on each other.
Indirect facilitation: one plant benefits neighboring plants such as by removing potential competitors, introducing beneficial organisms, or protecting its neighbors from pathogens, pests, herbivores, or parasites.
Intercropping: simultaneous growth of at least two crop species within the same field.
No-tillage: agricultural practice of growing crops or pasture without disturbing the soil.
Plant litter: dead plant material (such as leaves, needles, twigs, and root) that decomposes in the field.
Plant mixture: different plant species or varieties are grown simultaneously, or partly so, in the same field.

to the soil to decompose. Greater soil fertility may also result from lower nutrient-leaching losses from species-rich communities. Greater soil fertility enhances plant biomass production during the following year, creating a positive feedback loop with greater biomass inputs being added to the soil [15,41], thus strengthening the positive biodiversity–ecosystem productivity relationships over time.

Soil organic C (SOC) is a key indicator of soil fertility and soil quality and is linked to multiple processes, such as the retention and release of nutrients, and soil structure formation [42,43]. Plant litter in the form of dead shoots and roots is an important source of SOC in terrestrial ecosystems [14]. Increased productivity in species-diverse plant communities can enhance plant aboveground litterfall and root inputs to soils [26]. Greater plant diversity can increase soil C and N accumulation [41,44] through enhanced litter inputs, increasing microbial growth and turnover, and entombment of necromass [27,45,46].

Litter species diversity can also alter SOC accumulation, the retention and release of nutrients via diversity effects on litter quality, and decomposition processes (Figure 1, arrow b). Plant litter inputs and the decomposition process are two primary controls over C and N accumulation and nutrient release in soils [23,24]. Mixing litter from different species can accelerate (synergistic effects) or inhibit (antagonistic effects) decomposition compared with the average decomposition of the mixture components [23,28,47]. Various studies have suggested that non-additive effects (e.g., synergistic) are more common compared with additive effects in the decomposition of litter mixtures [24,25,48]. Synergistic effects might result from: (i) N transfer from species that produce high-quality litter to plants that produce low-quality litter; (ii) improvement in microenvironmental conditions; and (iii) complementary resource use among microbial decomposers or detritivores [24,48]. Conversely, antagonistic effects are often induced by the effect of specific components (e.g., polyphenols in one litter component), which inhibit microbial growth and activity of the whole community, and consequently impede decomposition of both litter types [48,49]. The soil C and N accumulation potential of a species mixture via enhanced litter input is partly counteracted by faster decomposition of litter mixtures. However, high-quality (i.e., rapidly decomposing) plant litter mixture inputs could enhance C storage through increased microbial growth, turnover, and microbial necromass accumulation over time [50]. Litter quality may be more important than microbial physiological traits in enhancing SOC storage in temperate forests [51].

Experimental evidence across four long-term intercropping experiments showed that intercropping enhanced soil C and N content, especially in infertile soils [6]. During the second period (13–22 years) of a grassland biodiversity experiment, the active restoration of high-diversity late-successional plant communities accelerated soil C accrual, with C storage accumulating at a rate 200% greater than the rate observed in a natural succession at the same site, and 70% greater than in monocultures [52]. A global meta-analysis indicated that positive plant diversity effects on SOC also increase over time [26]. Another meta-analysis showed that species diversity effects on soil N become more positive with the number of species in the mixture and with stand age because of enhanced feedback between litter inputs, decomposition rates, and soil biota, as well as reduced N leaching [34].

In addition to soil C and N, greater plant species diversity across very different ecosystems can contribute to the amelioration of soil biogeochemical properties through the greater input of soil K, calcium (Ca), and magnesium (Mg) [41], the enhancement of the soil total P bank and available soil P [53], and the formation of soil macroaggregates [6]. Changes in the quantity and quality of litter mixtures can directly or indirectly affect soil fertility properties in highly diverse plant mixtures.

Reduced tillage: tillage practice of minimizing soil disturbance and allowing crop residue or stubble to remain in the field.
Residue retention: crop residues left on the soil surface or incorporated into the soil by tillage.
Residue-borne or stubble-borne disease: crop diseases, which are mainly caused by pathogens that can overwinter on plant residues by carrying out a specific part of their life cycles, leading to the production of primary inoculum.
Selection effect: increased probability of having a species adapted to the given environmental conditions when more species are present in species mixtures.
Soil biodiversity: variety of life that exists within the soil, from genes to species and communities, as well as the ecological complexes of which they are part from soil microhabitats to landscapes.
Soil fertility: capability of soil to support plant biomass production by providing essential nutrients and favorable soil physical, chemical, and biological environmental conditions for plant growth.
Soil-borne pathogens: plant diseases caused by pathogens, which infect the host from the soil environment, rather than air or water.

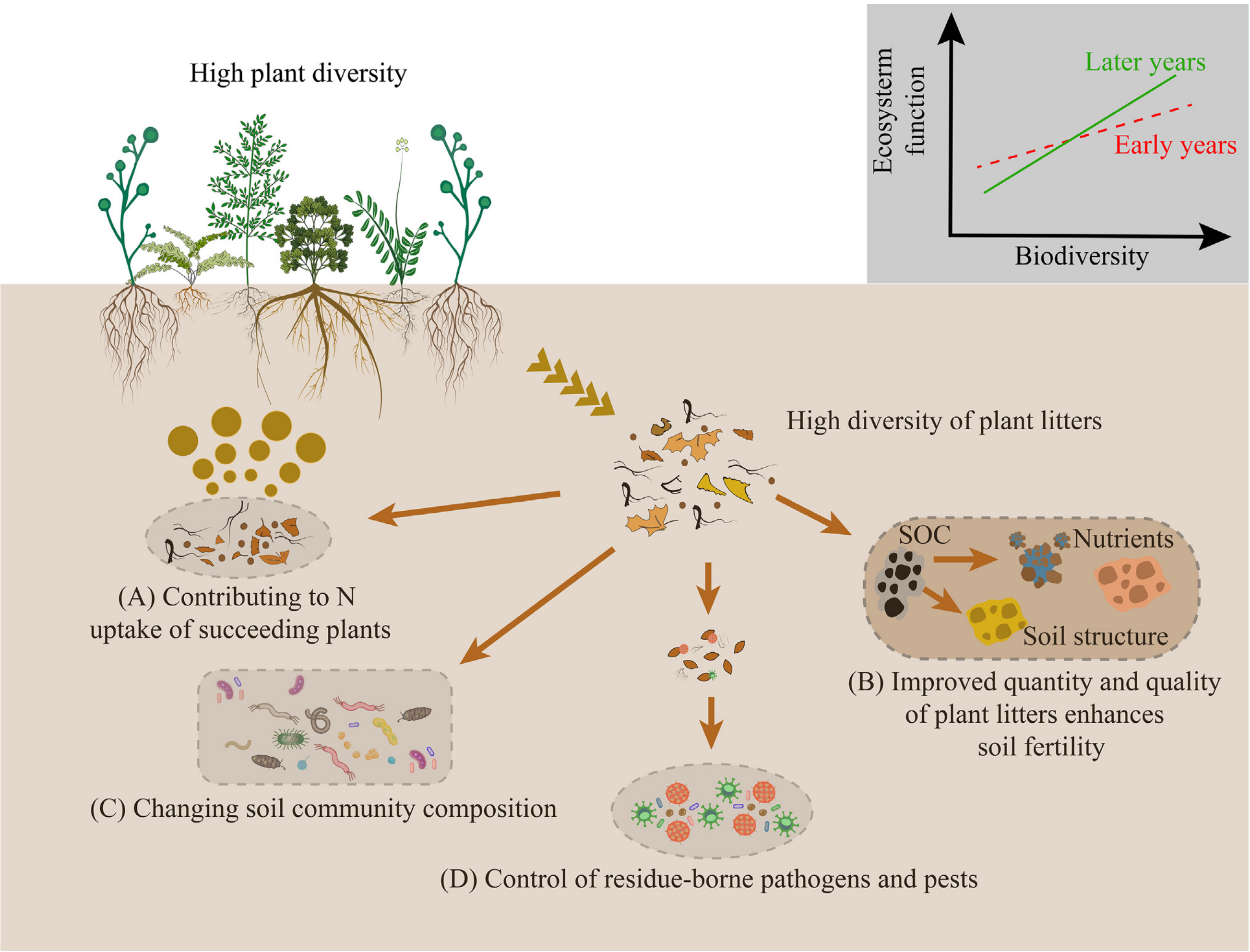


Figure 1. The role of plant litter in strengthening biodiversity and ecosystem functioning relationships over time via four pathways. (A) contribution of plant residue (especially from legumes) to the nitrogen (N) requirements of following plants (B) enhancing soil fertility; (C) changing soil community composition; and (D) controlling residue-borne pathogens and pests.

Altered soil community composition by diverse plant litter

The higher diversity of plant litter can increase the diversity of soil biota and change the composition of soil communities (Figure 1, arrow c; Figure 3A). In turn, soil biodiversity (bacteria, fungi, protists, and invertebrates) contributes significantly to shaping aboveground biodiversity and multiple ecosystem functions [54–56]. Plant species diversity can influence the soil food web via microhabitat diversity and the quantity and quality of plant litter returned to the soil (Figure 3A) [57–61]. Plant litter provides food, nutrients, and habitat for soil biota, thus influencing soil biodiversity and community structure [62,63]. A higher diversity of plant litter increases the diversity of soil decomposers, which in turn promotes the diversity of higher trophic levels within the soil food web [54,64]. Experimental studies using living plants and associated plant litter usually show positive effects of plant species diversity on the abundance, biomass, and activity of soil biota [20,65–67]. Multi-species litter mixtures had higher microbial abundance and fungal diversity than predicted from single-species litter in a Mediterranean shrubland [67]. Other studies

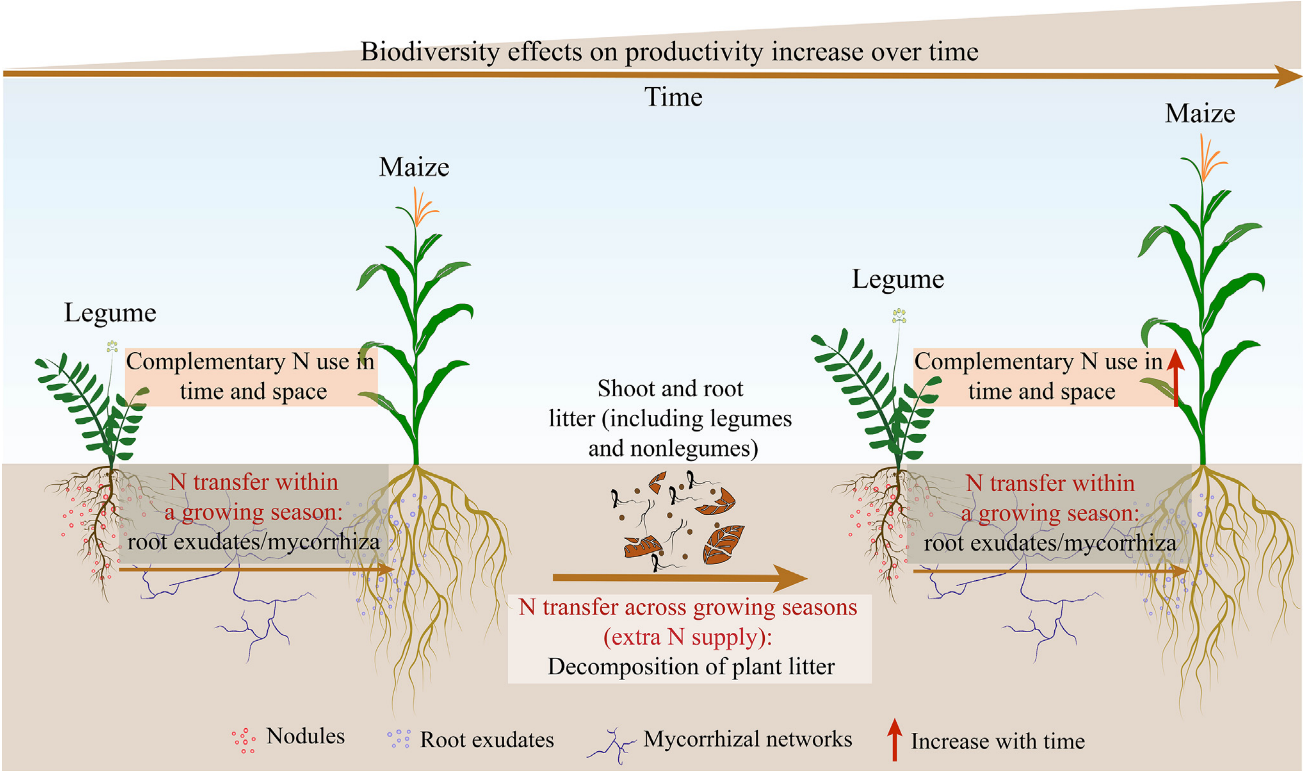
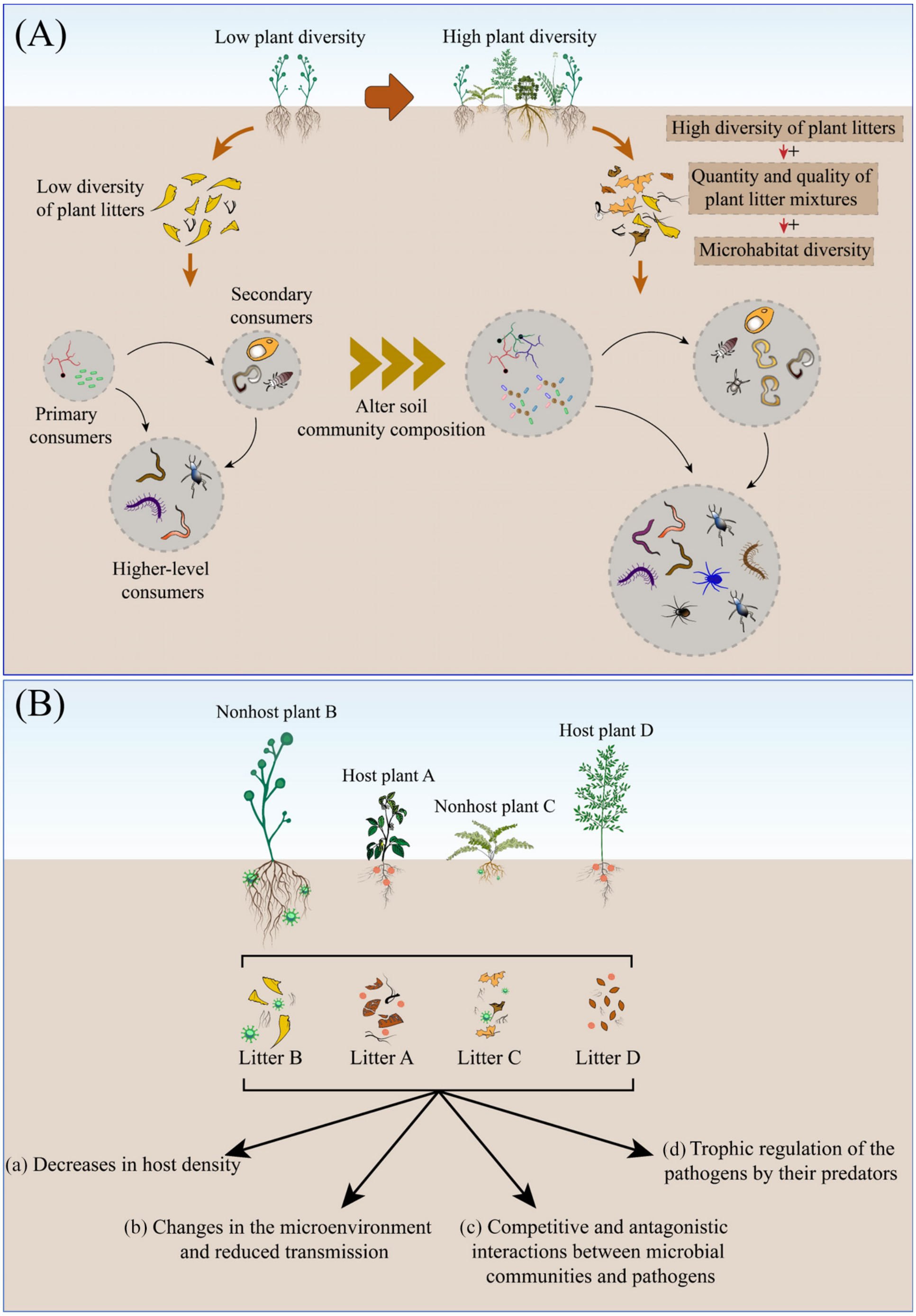


Figure 2. Belowground nitrogen (N) transfer from plant litter to succeeding plants can contribute to enhance the diversity effect over time. The decomposition of shoot and root litter (including legumes and nonlegumes) can provide extra N to plants in the following year. This extra N supply, together with complementary N use in time and space, and N transfer within a growing season in species mixtures, could help explain the stronger biodiversity effect on productivity over time.

suggest that litter diversity also influences soil community composition [68,69]. For example, mixing broad-leaf sassafras [*Sassafras tzumu* (Hemsl.) Hemsl.] with coniferous larch [*Larix kaempferi* (Lamb.) Carr.] litter decreased the abundance of the bacterial classes Acidobacteriia and Solibacteres while increasing that of the fungal class Dothideomycetes compared with larch litter [69]. Plant species identity or functional groups (e.g., legumes) are also important in influencing soil biota composition and functions [70]. Increasing evidence suggests that plant species or genotypic diversity has strong bottom-up effects on soil multitrophic interaction networks, in particular on primary consumers (microbes and plant feeders) rather than on secondary (microbe feeders) or tertiary consumers (predators) [58,71].

Studies that found weak or no plant diversity effects on soil organisms have been largely based on short-term experiments in which species richness effects may be due to the soil legacy effects of previous plant communities [64,72]. By contrast, long-term studies (≥6 years) found that the density and diversity of soil organisms showed a positive response to plant species richness after a time-lag of ~4 years [64,72]. Moreover, the effects of plant species diversity on nematode community composition and diversity increased over time, indicating time-lags of nematode responses to changes in plant diversity [64,66]. Changes in soil biodiversity and community composition in species-rich communities are largely due to microhabitat diversity, the accumulation of litter layers,



Trends in Ecology & Evolution

Figure 3. The role of diverse plant litter on the soil food web and biodiversity (A) and slowing the spread of residue-borne diseases and pests (B).

and inputs of root-derived resources [57–59,61]. We suggest that the effects of plant litter diversity on community composition and diversity of soil organisms increase over time, and this may contribute to strengthening BEF relationships over time.

The application of crop residues is the most effective practice for enhancing soil biodiversity in intensively managed agroecosystems [73,74]. For example, maize straw mulch is an important factor enhancing the abundance and diversity of soil mesofauna [74]. By increasing the quantity, quality, and chemical diversity of residues, high-diversity plant species rotations in agroecosystems can increase microbial community diversity and the relative abundance of fungi versus bacteria [75]. Intercropping can alter soil microbial community composition, as shown in three long-term field experiments [76]. Long-term maize/greenleaf desmodium (*Desmodium intortum*) and maize/silver-leaf desmodium (*Desmodium uncinatum*) intercropping diversified fungal microbiomes and favored taxa associated with plant productivity [77]. Since aboveground plant residues are generally removed from arable fields, more attention should be paid to the role of root residues, which might accumulate through time in long-term intercropping experiments and affect ecosystem functioning. We predict that diversified crop **residue retention** (including both shoot and root parts) contributes to increase soil biodiversity and influence soil community composition, with consequences for ecosystem functioning in diversified cropping systems (Box 1).

Diverse plant residues from species-rich ecosystems can control residue-borne pathogens and pests

Crop residues are the primary source of infection of many diseases for succeeding crops [11]. Thus, the conservation of crop residues in the field after harvest with **reduced-** or **no-tillage** practices may increase the risk of '**residue-borne**' or '**stubble-borne**' **disease** epidemics [78]. Diverse necrotrophic leaf-, stem-, and inflorescence-attacking fungal pathogens are known to survive on crop residues in the form of reproductive and spore-dissemination structures between cropping seasons [11]. For example, wheat pathogens, such as *Fusarium graminearum* and *Mycosphaerella graminicola*, survive on wheat residues and are likely to infect the next crop if the residues are left in the field after harvest [79]. Residues and old stems of sorghum and maize

Box 1. Optimizing plant residue retention in managed ecosystems

In-field retention of crop residues affects both crop productivity and soil fertility [74]. Straw (e.g., from maize, wheat, or rice) is often used for residue retention in monocultures, but our understanding of how to manage diverse straw retention in diversified cropping systems (e.g., intercropping) is limited. Integrated residue retention and **crop diversification** and soil tillage might better support agroecosystem functions over time.

Monoculture intensification can have detrimental effects on ecosystem functioning, whereas agricultural diversification can enhance ecosystem function [90,91], and some studies have indicated that crop residue management has an important role in ecosystem functions in diversified systems. For example, cover crops are usually killed and incorporated in soils by tillage, which can increase soil organic matter content [92]. In addition, the residues of some cover crops (e.g., brassicas) release volatile and toxic isothiocyanates during decomposition, and can suppress soil pests as **biofumigations** [93]. Furthermore, cover **crop mixtures** caused greater increases in SOC compared with mono-species cover crops, while adding legumes led to greater SOC increases compared with including only grass species [92].

Optimizing residue management aims to minimize negative impacts of the residue-borne disease while maximizing the benefit of residue nutrient to the following plants. Some crop residues are colonized by pathogens or can release autotoxic substances and may contribute to soil sickness [94]; removing these residues from fields is an important way to alleviate soil sickness. Crop residues affect pathogen control either directly or through associated soil tillage. A cropping system that includes zero tillage, crop rotations, and crop residue retention resulted in increased populations of soil microflora that promote plant growth and suppress diseases [95]. Thus, diversifying crop residue retention via residue mixtures (spatial scale) or sequential crop residue diversity (temporal scale) could reduce residue-borne pathogens in diversified cropping systems.

Agroecosystem diversification with legumes or nonlegumes improves ecosystem functions differently [96]. Legume-based crop residue retention in plant mixture can improve N uptake of succeeding crops in long-term diversified systems [36]. However, it is important to manage the timing of nutrient release from residue mixtures with the timing of succeeding crop nutrient demand, otherwise nutrients become vulnerable to loss through leaching [97]. Mixing legume with nonlegume residues is a potential strategy to regulate the rate of nutrient release rate [49].

left in the field contain large numbers of live larvae and constitute an important reservoir for infestation of lepidopterous stemborers [80]. Residue-borne pathogens and pests are different from **soil-borne pathogens** and pests in terms of overwintering habitat and possible pathogen control methods.

Diverse plant litter can help control residue-borne diseases and pests via: (i) decreases in host density; (ii) changes in the microenvironment and reduced transmission; (iii) interactions between plant-beneficial microbes and pathogens; and (iv) the effects of trophic regulation of the pathogens by their predators (Figure 1, arrow d; Figure 3B).

The host plant and litter density tends to decrease with increasing plant species richness, diluting pathogens and pests in high-diverse plant communities (Figure 3B, arrow a) [9,81]. Using soils collected from a 10-year crop-diversified field experiment, it was shown that faba bean monocultures accumulated more pathogens, whereas maize/faba bean intercropping increased the relative abundance of mutualistic rhizobia [82].

Diverse plant litter also changes the microenvironment in ways that physically block the dispersal and transmission of pathogens and pests (Figure 3B, arrow b) [83,84]. Plant litter from continuous monoculture cropping is conducive for pathogens and pests to continue their life cycle with no break, leading to rapid multiplication of pathogens, pests, and increased disease severity (i.e., **continuous cropping obstacle**). By contrast, residue-borne pathogens and pests can be controlled by appropriate intercropping or rotations with nonhost crops [78,85].

Competitive and antagonistic interactions between microbial communities and pathogens harbored in species-diverse litter mixtures tend to prevent the outbreak of pathogens (Figure 3B, arrow c) [11,86]. For example, incorporation of pineapple residues in the soil alleviated pathogen pressure by increasing the relative abundance of antagonistic fungal taxa that suppressed pathogen growth and *Fusarium* wilt disease incidence [87].

Finally, increased plant species and litter diversity can reduce the abundance of pathogens, pests, and their damage by promoting predator and parasitoid abundance (Figure 3B, arrow d) [54,64,88]. Specific residue-borne pathogens gradually accumulate in monocultures, with negative consequences for plant growth, whereas diverse plant-litter mixtures reduce the incidence and spread of residue-borne pathogens and pests in the long-term.

Concluding remarks

Plant diversity–productivity relationships become more positive over time; however, potential explanations for this have mainly focused on short-term interactions between living plants and the soil environment, and less on the long-term accumulation and decomposition of plant litter. We suggest four litter-mediated mechanisms that might contribute to these increasing positive effects (Figure 1). These four mechanisms may operate simultaneously with other ecological mechanisms and can vary greatly with climate, ecosystem, soil type, species identity, and field management (Box 2). There is also evidence that initial strong effects of species loss on biomass production in natural ecosystems may actually decrease and not increase over time [89]. A key challenge remains to disentangle long-term effects of litter-mediated processes from short-term effects of living plants and the soil environment across different ecosystems (see Outstanding questions). This will provide new insights into how plant diversity–productivity relationships may change over time in the face of environmental change. We suggest that the diversification of crop residue retention (including shoot and root parts) by varying either residue

Outstanding questions

How can we quantify the short- and long-term role of plant-litter mixtures in influencing ecosystem functioning through litter-removal experiments? The role of plant-litter mixtures needs to be demonstrated through implementation of litter-removal and/or addition experiments. Crop residue management is widely practiced across agroecosystems, but large-scale litter manipulations through litter removal or addition remain experimentally challenging in natural ecosystems.

How can we separate the ecosystem effects of plant litter from those of living plants and the soil environment? Litter-mediated mechanisms may operate simultaneously with short-term mechanisms associated with living plants and the soil environment in the long-term biodiversity experiments. Thus, biodiversity experiments should focus simultaneously on both short- and long-term mechanisms.

How can we quantify the contribution of root residues to strengthened ecosystem functions in species-diverse communities in the long-term? So far, most studies have focused on the role of aboveground litter on ecosystem functioning, while root decomposition may be more important in driving ecological processes, such as soil C and N cycling and soil biodiversity. Compared with shoot residues, the role of diverse root residues is often overlooked in long-term diversified cropping systems.

How do litter mixtures affect soil community composition and residue-borne pathogens over time? Plant diversity can influence soil food web and biodiversity via microhabitat diversity, and the quantity and quality of plant litter. In addition, plant diversity effects on soil biota diversity and pathogen suppression strengthen over time. We still lack direct experimental evidence of these potential long-term effects of diverse litter from plant mixtures on soil community composition and residue-borne pathogens.

How can we manage diverse plant residues and design more productive and sustainable cropping (e.g., intercropping and agroforestry) and seminatural systems (e.g., managed

Box 2. Role of plant litter in the short- and long-term

The role of plant litter in biodiverse plant communities can be relatively small in the short-term compared with the effects of living plants on ecosystem processes. However, plant litter is likely to have larger effects on ecosystem functions in the long-term (Figure I). The ‘subsequent uptake of previous N inputs’ is a gradual process [98]; for example, only 8.3% of wheat residue N was recovered in the succeeding wheat plants in a 2-year field experiment [99]. The only long-term tracer study available showed that the cumulative ^{15}N recovery by crops could still increase even 28 years after ^{15}N fertilization (Figure IA) [100]. In addition, the average annual nutrient release by previous plant residues tends to be negligible compared with the annual N fertilizer inputs over a long period [98]. Variations in soil fertility occur slowly, and significant changes in soil organic matter composition can only be detected through long-term observations (Figure IB) [45,52]. Previous studies have demonstrated that living plant diversity effects on soil biota diversity [64,72] and pathogen suppression [81] strengthen over time. In addition, diverse plant-litter mixtures are important in mediating living plant diversity effects on soil biodiversity [57–61] and residue-borne pathogen [78,85,87]. These results implied that the role of diverse plant-litter mixtures contributed to increasing soil biodiversity (Figure IC) and slowing the spread of residue-borne diseases increases over time in the long-term (Figure ID).

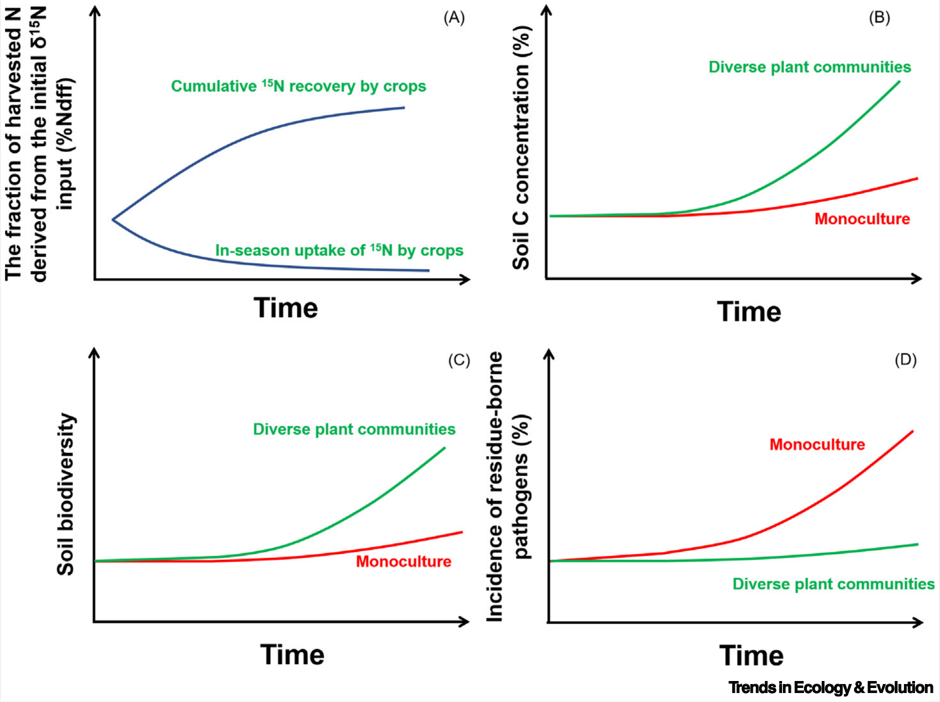


Figure I. Plant litter-mediated processes in long-term plant diversity experiments. The fraction of harvested nitrogen (N) derived from the initial $\delta^{15}N$ input by crops (A), change in soil C concentration (B), soil biodiversity (C), and incidence of residue-borne pathogens (D) in monocultures and diverse plant communities over time. Abbreviation: C, carbon.

mixtures (spatial scale) or sequential crop residue diversity (temporal scale) will be crucial to improve the sustainability of food production (e.g., intercropping and agroforestry) and seminatural systems (e.g., managed forests and sown grasslands)?

forests and sown grasslands)? Residue management is widely practiced in monocultures using aboveground crop residue (i.e., straw) of a single species (e.g., maize, wheat, or rice). Diverse cropping systems will produce diversified crop residues (including shoot and root parts), which could be managed to make agroecosystems more sustainable and resilient to environmental change.

Acknowledgments

We thank S.Y. Wu for her help with the figures. The study was financially supported by the Natural Science Foundation of China (32130067, 31971450, and 31500348) and the National Key Research and Development Program of China (2022YFD1500702 and 2022YFC3501503). R.M.C. thanks the USA National Science Foundation EPSCoR Cooperative Agreement OIA-1757351 for support.

Declaration of interests

None declared by authors.

References

1. Reich, P.B. *et al.* (2012) Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336, 589–592
2. Huang, Y. *et al.* (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362, 80–83
3. Bongers, F.J. *et al.* (2021) Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nat. Ecol. Evol.* 5, 1594–1603
4. Urgoiti, J. *et al.* (2022) No complementarity no gain—net diversity effects on tree productivity occur once complementarity emerges during early stand development. *Ecol. Lett.* 25, 851–862
5. Zhang, W.-P. *et al.* (2021) Shifts from complementarity to selection effects maintain high productivity in maize/legume intercropping systems. *J. Appl. Ecol.* 58, 2603–2613
6. Li, X.-F. *et al.* (2021) Long-term increased grain yield and soil fertility from intercropping. *Nat. Sustain.* 4, 943–950
7. 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
8. Guerrero-Ramírez, N.R. *et al.* (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* 1, 1639–1642
9. 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
10. Zuppinger-Dingley, D. *et al.* (2014) Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515, 108–111
11. Kerdraon, L. *et al.* (2019) Differential dynamics of microbial community networks help identify microorganisms interacting with residue-borne pathogens: the case of *Zymoseptoria tritici* in wheat. *Microbiome* 7, 1–17
12. Datry, T. *et al.* (2018) A global analysis of terrestrial plant litter dynamics in non-perennial waterways. *Nat. Geosci.* 11, 497–503
13. Lal, R. (2005) World crop residues production and implications of its use as a biofuel. *Environ. Int.* 31, 575–584
14. Dijkstra, F.A. *et al.* (2021) Root effects on soil organic carbon: a double-edged sword. *New Phytol.* 230, 60–65
15. Hobbie, S.E. (2015) Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends Ecol. Evol.* 30, 357–363
16. Veen, G. *et al.* (2019) The role of plant litter in driving plant–soil feedbacks. *Front. Environ. Sci.* 7, 168
17. Feng, J. *et al.* (2022) Changes in plant inputs alter soil carbon and microbial communities in forest ecosystems. *Glob. Chang. Biol.* 28, 3426–3440
18. Zhang, Z. *et al.* (2021) Effect of allelopathy on plant performance: a meta-analysis. *Ecol. Lett.* 24, 348–362
19. Ganade, G. and Brown, V.K. (2002) Succession in old pastures of central Amazonia: role of soil fertility and plant litter. *Ecology* 83, 743–754
20. Wang, W. *et al.* (2020) Effects of mixed-species litter on bacterial and fungal lignocellulose degradation functions during litter decomposition. *Soil Biol. Biochem.* 141, 107690
21. Ma, Z. *et al.* (2022) Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Funct. Ecol.* 36, 148–158
22. Wright, A.J. *et al.* (2017) The overlooked role of facilitation in biodiversity experiments. *Trends Ecol. Evol.* 32, 383–390
23. Porre, R.J. *et al.* (2020) Is litter decomposition enhanced in species mixtures? A meta-analysis. *Soil Biol. Biochem.* 145, 107791
24. Kou, L. *et al.* (2020) Diversity–decomposition relationships in forests worldwide. *eLife* 9, e55813
25. Mori, A.S. *et al.* (2020) A meta-analysis on decomposition quantifies afterlife effects of plant diversity as a global change driver. *Nat. Commun.* 11, 4547
26. Chen, X. *et al.* (2020) Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biol. Rev.* 95, 167–183
27. Chen, S. *et al.* (2018) Plant diversity enhances productivity and soil carbon storage. *Proc. Natl. Acad. Sci. U. S. A.* 115, 4027–4032
28. Handa, I.T. *et al.* (2014) Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509, 218–221
29. Peoples, M.B. *et al.* (2015) Can differences in ^{15}N natural abundance be used to quantify the transfer of nitrogen from legumes to neighbouring non-legume plant species? *Soil Biol. Biochem.* 87, 97–109
30. Coskun, D. *et al.* (2017) How plant root exudates shape the nitrogen cycle. *Trends Plant Sci.* 22, 661–673
31. Dierks, J. *et al.* (2022) Mycorrhizal fungi-mediated uptake of tree-derived nitrogen by maize in smallholder farms. *Nat. Sustain.* 5, 64–70
32. Fustec, J. *et al.* (2010) Nitrogen rhizodeposition of legumes. A review. *Agron. Sustain. Dev.* 30, 57–66
33. Thilakarathna, M.S. *et al.* (2016) Belowground nitrogen transfer from legumes to non-legumes under managed herbaceous cropping systems. A review. *Agron. Sustain. Dev.* 36, 1–16
34. Chen, X. *et al.* (2021) Negative to positive shifts in diversity effects on soil nitrogen over time. *Nat. Sustain.* 4, 225–232
35. Zhao, J. *et al.* (2022) Global systematic review with meta-analysis reveals yield advantage of legume-based rotations and its drivers. *Nat. Commun.* 13, 4926
36. Li, X. *et al.* (2015) Quantifying biological nitrogen fixation of different catch crops, and residual effects of roots and tops on nitrogen uptake in barley using in-situ ^{15}N labelling. *Plant Soil* 395, 273–287
37. Trannin, W.S. *et al.* (2000) Interspecies competition and N transfer in a tropical grass-legume mixture. *Biol. Fertil. Soils* 32, 441–448
38. 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
39. Noack, S.R. *et al.* (2014) Management of crop residues affects the transfer of phosphorus to plant and soil pools: results from a dual-labelling experiment. *Soil Biol. Biochem.* 71, 31–39
40. Liao, D. *et al.* (2022) Adding intercropped maize and faba bean root residues increases phosphorus bioavailability in a calcareous soil due to organic phosphorus mineralization. *Plant Soil* 476, 201–218
41. Furey, G.N. and Tilman, D. (2021) Plant biodiversity and the regeneration of soil fertility. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2111321118
42. Kopittke, P.M. *et al.* (2022) Ensuring planetary survival: the centrality of organic carbon in balancing the multifunctional nature of soils. *Crit. Rev. Environ. Sci. Technol.* 52, 4308–4324
43. Qiao, L. *et al.* (2022) Soil quality both increases crop production and improves resilience to climate change. *Nat. Clim. Change* 12, 574–580
44. Lange, M. *et al.* (2015) Plant diversity increases soil microbial activity and soil carbon storage. *Nat. Commun.* 6, 6707
45. Lange, M. *et al.* (2019) How plant diversity impacts the coupled water, nutrient and carbon cycles. *Adv. Ecol. Res.* 61, 185–219
46. Bai, Y. and Cotrufo, M.F. (2022) Grassland soil carbon sequestration: current understanding, challenges, and solutions. *Science* 377, 603–608
47. Grossman, J.J. *et al.* (2020) Functional diversity of leaf litter mixtures slows decomposition of labile but not recalcitrant carbon over two years. *Ecol. Monogr.* 90, e01407
48. Hättenschwiler, S. *et al.* (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 36, 191–218
49. Liu, J. *et al.* (2020) Synergistic effects: a common theme in mixed-species litter decomposition. *New Phytol.* 227, 757–765
50. Sokol, N.W. and Bradford, M.A. (2019) Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nat. Geosci.* 12, 46–53

51. Craig, M.E. *et al.* (2022) Fast-decaying plant litter enhances soil carbon in temperate forests but not through microbial physiological traits. *Nat. Commun.* 13, 1229
52. Yang, Y. *et al.* (2019) Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nat. Commun.* 10, 1–7
53. Chen, X. *et al.* (2022) Meta-analysis shows that plant mixtures increase soil phosphorus availability and plant productivity in diverse ecosystems. *Nat. Ecol. Evol.* 6, 1112–1121
54. Delgado-Baquerizo, M. *et al.* (2020) Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat. Ecol. Evol.* 4, 210–220
55. Bardgett, R.D. and van der Putten, W.H. (2014) Belowground biodiversity and ecosystem functioning. *Nature* 515, 505–511
56. Guerra, C.A. *et al.* (2021) Tracking, targeting, and conserving soil biodiversity. *Science* 371, 239–241
57. Barnes, A. *et al.* (2020) Biodiversity enhances the multitrophic control of arthropod herbivory. *Sci. Adv.* 6, eabb6603
58. Scherber, C. *et al.* (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468, 553–556
59. Sokol, N.W. *et al.* (2022) Life and death in the soil microbiome: how ecological processes influence biogeochemistry. *Nat. Rev. Microbiol.* 20, 415–430
60. Zhao, C. *et al.* (2021) Considerable impacts of litter inputs on soil nematode community composition in a young *Acacia crassicapa* plantation. *Soil Ecol. Lett.* 3, 145–155
61. Chen, C. *et al.* (2019) Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. *Nat. Commun.* 10, 1332
62. Yan, J. *et al.* (2018) Plant litter composition selects different soil microbial structures and in turn drives different litter decomposition pattern and soil carbon sequestration capability. *Geoderma* 319, 194–203
63. Fujii, S. *et al.* (2020) Living litter: dynamic trait spectra predict fauna composition. *Trends Ecol. Evol.* 35, 886–896
64. 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
65. Eisenhauer, N. *et al.* (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6889–6894
66. Dietrich, P. *et al.* (2021) Effects of plant species diversity on nematode community composition and diversity in a long-term biodiversity experiment. *Oecologia* 197, 297–311
67. Santonja, M. *et al.* (2017) Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland. *Soil Biol. Biochem.* 111, 124–134
68. Zhang, W. *et al.* (2019) Microbial groups and their functions control the decomposition of coniferous litter: a comparison with broadleaved tree litters. *Soil Biol. Biochem.* 133, 196–207
69. Wang, W. *et al.* (2019) Impacts of mixed litter on the structure and functional pathway of microbial community in litter decomposition. *Appl. Soil Ecol.* 144, 72–82
70. Fanin, N. *et al.* (2019) Effects of plant functional group removal on structure and function of soil communities across contrasting ecosystems. *Ecol. Lett.* 22, 1095–1103
71. Yan, J. *et al.* (2021) Plant genotypic diversity effects on soil nematodes vary with trophic level. *New Phytol.* 229, 575–584
72. Jongen, R. *et al.* (2021) Plant community legacy effects on nutrient cycling, fungal decomposer communities and decomposition in a temperate grassland. *Soil Biol. Biochem.* 163, 108450
73. Liu, C. *et al.* (2020) Soil bacterial diversity and potential functions are regulated by long-term conservation tillage and straw mulching. *Microorganisms* 8, 836
74. Jiang, Y. *et al.* (2021) Relationship between the amounts of surface corn stover mulch and soil mesofauna assemblage varies with the season in cultivated areas of northeastern China. *Soil Tillage Res.* 213, 105091
75. Tiemann, L. *et al.* (2015) Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecol. Lett.* 18, 761–771
76. Tian, X.-l. *et al.* (2019) Crop diversity facilitates soil aggregation in relation to soil microbial community composition driven by intercropping. *Plant Soil* 436, 173–192
77. Mwakilili, A.D. *et al.* (2021) Long-term maize-*Desmodium* intercropping shifts structure and composition of soil microbiome with stronger impact on fungal communities. *Plant Soil* 467, 437–450
78. Kerdraon, L. *et al.* (2019) Crop residues in wheat-oilseed rape rotation system: a pivotal, shifting platform for microbial meetings. *Microb. Ecol.* 77, 931–945
79. Aboukhaddour, R. *et al.* (2020) Wheat diseases on the prairies: a Canadian story. *Plant Pathol.* 69, 418–432
80. Taddele, A. *et al.* (2020) Crop injury and yield losses in maize by the African maize stem borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) in Southern Ethiopia. *Int. J. Pest Manage* Published online December 18, 2020. https://doi.org/10.1080/09670874.2020.1861360
81. Thakur, M.P. *et al.* (2021) Plant–soil feedbacks and temporal dynamics of plant diversity–productivity relationships. *Trends Ecol. Evol.* 36, 651–661
82. Wang, G. *et al.* (2021) Soil microbial legacy drives crop diversity advantage: linking ecological plant–soil feedback with agricultural intercropping. *J. Appl. Ecol.* 58, 496–506
83. Zhang, C. *et al.* (2019) Intercropping cereals with faba bean reduces plant disease incidence regardless of fertilizer input; a meta-analysis. *Eur. J. Plant Pathol.* 154, 931–942
84. Zhu, Y. *et al.* (2000) Genetic diversity and disease control in rice. *Nature* 406, 718–722
85. Giles, J.M. *et al.* (2022) Management strategies and distribution of *Aphanomyces* root rot of alfalfa (*Medicago sativa*), a continuing threat to forage production in the United States. *Plant Pathol.* 71, 1231–1240
86. Li, M. *et al.* (2019) Facilitation promotes invasions in plant-associated microbial communities. *Ecol. Lett.* 22, 149–158
87. Yuan, X. *et al.* (2021) Development of fungal-mediated soil suppressiveness against *Fusarium* wilt disease via plant residue manipulation. *Microbiome* 9, 200
88. Wan, N.-F. *et al.* (2020) Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nat. Plants* 6, 503–510
89. Kardol, P. *et al.* (2018) Long-term effects of species loss on community properties across contrasting ecosystems. *Nature* 557, 710–713
90. Tamburini, G. *et al.* (2020) Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci. Adv.* 6, eaba1715
91. Beillouin, D. *et al.* (2021) Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Glob. Chang. Biol.* 27, 4697–4710
92. Jian, J. *et al.* (2020) A meta-analysis of global cropland soil carbon changes due to cover cropping. *Soil Biol. Biochem.* 143, 107735
93. Morris, E.K. *et al.* (2020) Effective methods of biofumigation: a meta-analysis. *Plant Soil* 446, 379–392
94. Huang, L.-F. *et al.* (2013) Plant-soil feedbacks and soil sickness: from mechanisms to application in agriculture. *J. Chem. Ecol.* 39, 232–242
95. Govaerts, B. *et al.* (2006) Long-term consequences of tillage, residue management, and crop rotation on maize/wheat root rot and nematode populations in subtropical highlands. *Appl. Soil Ecol.* 32, 305–315
96. Sauvadet, M. *et al.* (2021) Agroecosystem diversification with legumes or non-legumes improves differently soil fertility according to soil type. *Sci. Total Environ.* 795, 148934
97. De Notaris, C. *et al.* (2019) Manipulating cover crop growth by adjusting sowing time and cereal inter-row spacing to enhance residual nitrogen effects. *Field Crops Res.* 234, 15–25
98. Quan, Z. *et al.* (2021) Different quantification approaches for nitrogen use efficiency lead to divergent estimates with varying advantages. *Nat. Food* 2, 241–245
99. Li, F. *et al.* (2015) Fate of nitrogen from green manure, straw, and fertilizer applied to wheat under different summer fallow management strategies in dryland. *Biol. Fertil. Soils* 51, 769–780
100. Sebilo, M. *et al.* (2013) Long-term fate of nitrate fertilizer in agricultural soils. *Proc. Nat. Acad. Sci. U. S. A.* 110, 18185–18189