

# Functional diversity of microbial decomposers facilitates plant coexistence in a plant–microbe–soil feedback model

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Theory and empirical evidence suggest that plant–soil feedback (PSF) determines the structure of a plant community and nutrient cycling in terrestrial ecosystems. The plant community alters the nutrient pool size in soil by affecting litter decomposition processes, which in turn shapes the plant community, forming a PSF system. However, the role of microbial decomposers in PSF function is often overlooked, and it remains unclear whether decomposers reinforce or weaken litter-mediated plant control over nutrient cycling. Here, we present a theoretical model incorporating the functional diversity of both plants and microbial decomposers. Two fundamental microbial processes are included that control nutrient mineralization from plant litter: (i) assimilation of mineralized nutrient into the microbial biomass (microbial immobilization), and (ii) release of the microbial nutrients into the inorganic nutrient pool (net mineralization). With this model, we show that microbial diversity may act as a buffer that weakens plant control over the soil nutrient pool, reversing the sign of PSF from positive to negative and facilitating plant coexistence. This is explained by the decoupling of litter decomposability and nutrient pool size arising from a flexible change in the microbial community composition and decomposition processes in response to variations in plant litter decomposability. Our results suggest that the microbial community plays a central role in PSF function and the plant community structure. Furthermore, the results strongly imply that the plant-centered view of nutrient cycling should be changed to a plant–microbe–soil feedback system, by incorporating the community ecology of microbial decomposers and their functional diversity.

buffering effect | ecological model | microbial community | nutrient cycling | plant–soil feedback

There is a long-standing view that a plant controls the soil conditions (e.g., size of inorganic nutrient pool) via litter supply in terrestrial ecosystems. On the basis of this view, a plant community and local soil conditions are understood as an outcome of the plant–soil codevelopment process. A change in the composition of a plant community leads to a change in litter quality, which alters the local nutrient cycling process and soil conditions; the changed soil conditions may in turn drive a further change in plant community composition. Those two processes taken together form a plant–soil feedback (PSF), a major driver of plant community dynamics and nutrient cycling [1, 2 (and references therein), 3].

Litter quality is a key plant trait that determines whether PSF supports or inhibits the coexistence of plant species. Both empirical (4–6) and theoretical (7–9) evidence indicate that litter-mediated PSF from the dominant species in a plant community can be positive (favoring species dominance) or negative (favoring competitor invasion), depending on the combinations of litter quality and nutrient competition strategy. If the dominant species favors nutrient-rich sites and produces a quickly decomposing litter, then the accelerated nutrient cycling maintains a competitive advantage, preventing competitor invasion and enhancing species dominance (8). Species dominance is also maintained when a species favors nutrient-poor sites and produces a slowly decomposing litter, leading to diminished nutrient cycling. With other combinations

[i.e., species with a competitive advantage in nutrient-rich (or -poor) sites with a poorly (or easily) decomposing litter], plant control on nutrient cycling facilitates competitor invasion and accelerates succession (8).

Earlier studies concerning nutrient cycling PSF often neglected the roles of microbial decomposers in controlling the soil nutrient pool size, except some studies on microbial pathogens and symbionts that directly interact with plants (10–15). However, recent studies in microbial ecology have started to challenge this plant-centered view of plant–soil systems. Two specific lines of evidence suggest that microbial decomposers can modify litter-mediated PSF. First, empirical evidence indicates that direct control of the nutrient pool size by the plant litter can be weak (16–18) because nutrients such as nitrogen within the plant litter are first assimilated into a microbial biomass or soil organic matter (immobilization) (19) and then released into the pool available for plants (net mineralization). Second, recent advances in culture-independent techniques indicate that microbial communities exhibit distinct compositions (20–25) and/or functions (21–23, 25, 26), depending on the litter quality and plant species with which they are associated. It has been hypothesized that flexibility in the community composition and function of microbial decomposers either reinforces (14, 27, 28) or weakens (3, 18) plant control over nutrient mineralization, although direct evidence for either hypothesis is lacking.

Here, using a simple mechanistic model for plant–microbe–soil feedback (PMSF), we show that incorporation of the soil microbial community poses a significant effect on the plant–soil codevelopment process. More specifically, microbial diversity provides the microbial community with a functional flexibility that buffers changes in the decomposability and thus weakens the plant control over nutrient cycling. Furthermore, the microbial diversity tends to shift the sign of PMSF from positive to negative and thus may facilitate plant coexistence.

## Model

Consider a plant community in a habitat comprising numerous discrete patches, each of which is either empty or is occupied by an individual of either of two plant species, a “better competitor for light” ( $P_L$ ) or a “better competitor for nutrient” ( $P_N$ ). The proportion of patches occupied by either species changes with time because of interpatch recruitment and within-patch mortality. Interpatch recruitment increases with the soil nutrient pool size ( $N$ ) through increased fecundity and/or increased seedling survival rate. The plant species  $P_L$  and  $P_N$  are representatives of plant

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groups with contrasting strategies (29). A modified patch occupancy model enables us to simulate shifts in the plant community composition along a gradient of soil nutrient pool sizes (8). The better competitor for nutrient  $P_N$  loses its competitive advantage and decreases its population size with increasing nutrient pool size. In contrast, the better competitor for light  $P_L$  increases its population size and dominates the habitat in nutrient-rich conditions.

Nutrients assimilated by the plants are released to the environment as plant litter (organic matter), which is decomposed by microbes. The mineralized nutrients are released to the nutrient pool, forming a nutrient cycling process (Fig. 1). Plant litter (detritus) consists of two organic compounds: “readily decomposable organic nutrient” ( $D_R$ ) and “slowly decomposable organic nutrient” ( $D_S$ ). The fractions of  $D_R$  in the litter from  $P_L$  and  $P_N$  are  $f_L$  and  $f_N$ , respectively. Litter with a higher  $D_R$  fraction (i.e., higher litter decomposability) is decomposed more rapidly by microbial decomposers.

It is reasonable to divide the whole microbial community into two contrasting functional groups (e.g., bacteria vs. fungi, or sugar fungi vs. cellulolytic fungi) that differ in their performance of the two organic nutrients (27, 30). “ $D_R$ -preferring microbes” ( $M_R$ ) and “ $D_S$ -preferring microbes” ( $M_S$ ) are better competitors for readily and slowly decomposable organic nutrient, respectively (i.e., functional complementarity) (Fig. 1). We assume that  $k_{Rm} > k_{Sm}$  represents the difference in litter quality ( $m = R$  or  $S$ ) and that  $k_{RR} > k_{RS}$  and  $k_{SR} < k_{SS}$  represent the functional complementarity (31, 32), where  $k_{jm}$  is the decomposition coefficient of  $D_j$  by  $M_m$  ( $j, m = R$  or  $S$ ; Methods). The assimilation efficiency ( $e_{Mj}$ ) is the fraction of mineralized organic nutrient that is assimilated into a biomass of  $M_j$  ( $j = R$  or  $S$ ) (i.e., microbial im-

mobilization), and  $1 - e_{Mj}$  is the fraction released to the nutrient pool (i.e., net mineralization). We assume a per-capita group-specific mortality ( $m_{Mj}$ ) due to predation for each group ( $j = R$  or  $S$ ). Nutrients in the microbial biomass are also released to the nutrient pool via this mortality (27). Major nutrient fluxes in our model are shown in Fig. 1, the model equations are shown in Methods, and a list of parameters and their default values are found in Table S1. Although we did not explicitly include microbe predators, the following results are qualitatively robust irrespective of complexities in the microbial food webs under reasonable assumptions (Fig. S1).

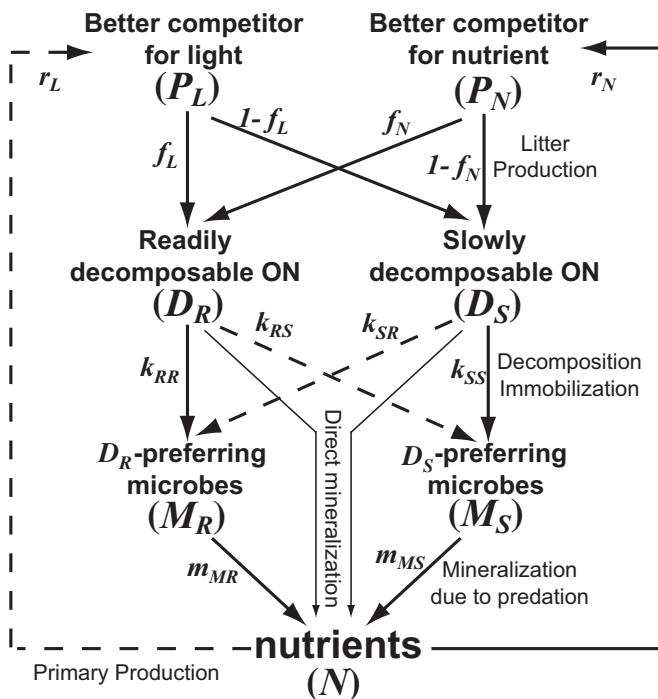
## Results

**Plant–Soil Feedbacks Along the Nutrient Gradient.** In our simple model, the nutrient pool size  $N^*$  at steady state is the key determinant of the sign of PSF (8). When the better competitor for light  $P_L$  is dominant in the plant community, it prevents (or allows) the invasion of the better competitor for nutrient  $P_N$  if the nutrient pool size is larger (or smaller) than  $\frac{r_N}{r_L} \frac{m_P}{r_L} (\equiv N_L^{**})$ , where  $m_P$  represents the per-capita mortality rate of individual plants. This is defined as positive (or negative) PSF in this model. Conversely, when  $P_N$  is dominant, it prevents (or allows) the invasion of  $P_L$  if the nutrient pool size is smaller (or larger) than  $\frac{m_P}{r_L} (\equiv N_N^{**})$ , which is defined as positive (or negative) PSF. Therefore, the plant litter decomposability, which affects the nutrient recycling rate and thus the size of the soil nutrient pool, potentially affects the sign of PSF.

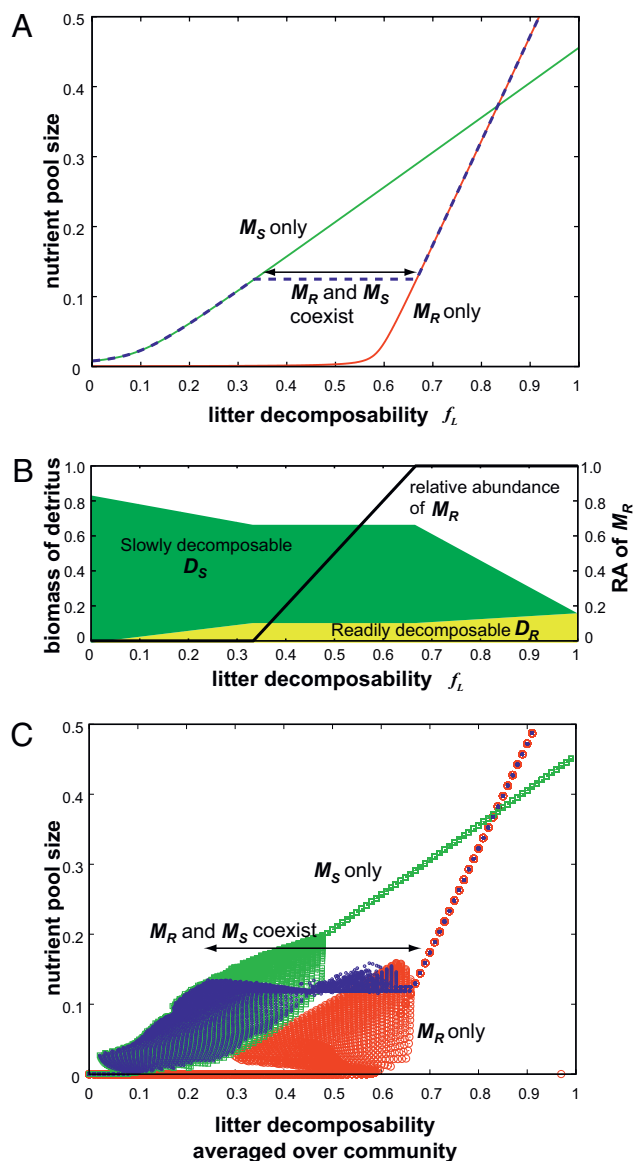
## Roles of Microbial Diversity in Plant Litter Control over Nutrient Cycling.

In the absence of microbial diversity, a higher litter decomposability simply leads to a larger nutrient pool size, regardless of the dominant microbial group. This is well demonstrated in a system in which a single plant species  $P_L$  is dominant with a single microbial group ( $M_R$  and  $M_S$  for the red and green lines in Fig. 2A, respectively). This pattern agrees with the long-standing view that plant litter decomposability determines the nutrient pool size (1–3). However, this is no longer true when microbial diversity is considered; the dependence of the nutrient pool size on litter decomposability is much weaker in the presence of two microbial groups (blue broken line in Fig. 2A:  $0.33 < f_L < 0.66$ ) than it is when microbial diversity is not considered (red and green lines in Fig. 2A).

The decoupling of the litter decomposability and nutrient pool size is achieved by the flexible shift of the microbial community composition and mineralization process in response to variations in the plant litter decomposability. Low litter decomposability favors microbes  $M_S$ , which prefer slowly decomposable  $D_S$  [relative abundance (RA) of  $M_R = M_R/(M_R + M_S)$ , RA of  $M_R = 0$  in Fig. 2B], whereas  $D_R$ -preferring microbes  $M_R$  are dominant when the litter decomposability is high (RA of  $M_R = 1$  in Fig. 2B). The two microbial groups coexist at equilibrium ( $0 < \text{RA of } M_R < 1$ ) at intermediate litter decomposability levels ( $0.33 < f_L < 0.66$ ), owing to the well-balanced supply of the two organic nutrient types (see SI Text, Section 1 and Tables S2 and S3 for the exact condition). In consequence of the competition between two microbes for two different types of organic nutrients, a higher plant litter decomposability (i.e., increased fraction of  $D_R$  in plant litter) leads to a higher relative abundance of  $D_R$ -preferring microbes  $M_R$  (Fig. 2B). This flexibility in microbial community composition alters the accumulation pattern of readily decomposable  $D_R$  and slowly decomposable  $D_S$  in a way that decouples litter decomposability and nutrient pool size (Fig. 2B). When a single microbial group dominates the community with a very high or very low litter decomposability ( $f_L < 0.33$  or  $f_L > 0.66$  in Fig. 2B), the total amount of accumulated organic nutrients ( $D_R + D_S$ ) decreases with an increasing supply of the readily decomposable fraction ( $D_R$ ) in the plant litter (i.e., higher litter



**Fig. 1.** Flow diagram of the plant–microbe–soil feedback model. Flows from the inorganic nutrient pool ( $N$ ) to the plant compartments ( $P_L$  and  $P_N$ ) represent primary production processes. Flows from the plant compartments to the two litter compartments ( $D_R$  and  $D_S$ ) represent litter production. Flows from the litter compartments to the microbial biomass ( $M_R$  and  $M_S$ ) represent decomposition (gross mineralization) and subsequent microbial immobilization (microbial growth) processes. Flows from the litter compartments to the inorganic nutrient pool represent direct mineralization. Flows from the microbial biomass to the inorganic nutrient pool represent net mineralization through nutrient release from microbial biomass due to predation.



**Fig. 2.** Consequences of PMSF on nutrient cycling, as a function of plant litter decomposability. (A) Relationship between litter decomposability ( $f_L$ ) and equilibrium nutrient pool size in systems with a better competitor for light ( $P_L$ ) only. Red, green, and blue lines correspond to systems with only  $M_R$ , only  $M_S$ , and both  $M_R$  and  $M_S$ , respectively. In the region with coexisting  $M_R$  and  $M_S$ , the slope of the line is zero. (B) Relationship between litter decomposability ( $f_L$ ), relative abundance of  $D_R$ -preferring microbes (RA of  $M_R$ , dimensionless), and readily decomposable  $D_R$  and slowly decomposable  $D_S$  accumulations in a system with  $P_L$  only. (C) Relationship between the average litter decomposability (long-term average of  $\frac{P_L f_L + F_N f_N}{P_L + F_N}$ , from  $t = 45,000$  to  $t = 50,000$ ) and the average nutrient pool size (long-term average of  $N$ ) in a system with two plant species. Consequences of PMSF on nutrient pool size for every combination of ( $f_L$  and  $f_N$ ) from (0.0, 0.0) to (1.0, 1.0) with interval ( $\Delta f_L, \Delta f_N$ ) = (0.01, 0.01) are plotted against the average litter decomposability in a system with microbial functional group  $M_R$  only (red dots),  $M_S$  only (green dots), and with two competing microbial groups (blue dots). All parameters are set as default values (Table S1).

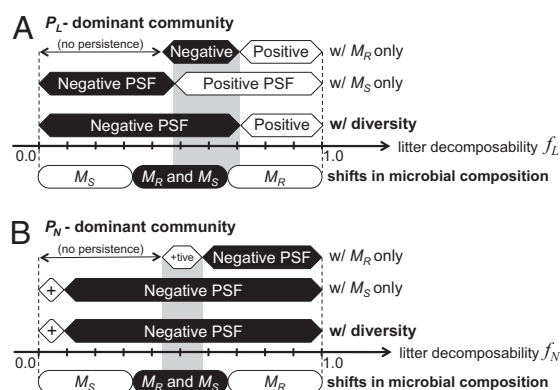
decomposability  $f_L$ ), leading to a larger nutrient pool size (Fig. 2A). However, when  $D_R$ - and  $D_S$ -preferring microbes coexist ( $0.33 < f_L < 0.66$ ), the amount of accumulated organic nutrient remains constant despite increases in the litter decomposability (Fig. 2B). The increase in  $D_R$ -preferring microbes ( $M_R$ ) allows rapid decomposition of the readily decomposable organic nutri-

ent fraction, preventing an increase in  $D_R$  accumulation. At the same time, the reduction in  $D_S$ -preferring microbes ( $M_S$ ) causes slower decomposition of the slowly decomposable fraction, resulting in the same level of  $D_S$  accumulation despite the increased litter decomposability. Therefore, the increase in litter decomposability does not increase the nutrient pool size (Fig. 2A).

Decoupling of the litter decomposability and the nutrient pool size is observed even when we assume differences in the mortalities of the microbial groups (Fig. S24) or a more complex soil food web structure (Fig. S1). When we consider a full system comprising two plant species and two microbial groups, the link that develops between the average litter decomposability of the plant community and the realized nutrient pool size becomes weaker in the presence of microbial diversity (Fig. 2C). In the region where the two microbes coexist, the realized nutrient pool size tends to be intermediate between those realized in the two systems without microbial diversity (i.e., between that realized with the dominance of  $M_S$  and that realized with the dominance of  $M_R$ ) (Fig. 2C).

**Roles of Microbial Diversity in Determining the Sign of PSF.** Consider a system comprising a single plant species in the absence of microbial diversity. When  $P_L$  produces a litter with sufficiently high decomposability  $f_L$ , it leads to a large nutrient pool size ( $>N_L^{**}$ ), causing a positive PSF (Fig. 3A). The threshold litter decomposability, which separates negative and positive PSF, depends on which microbial group dominates the community. When  $P_N$  is dominant, the sign of PSF is positive if its litter decomposability  $f_N$  is lower than a certain threshold (which depends on the microbial community composition), leading to a small nutrient pool size ( $<N_N^{**}$ ) (Fig. 3B). The buffering of the nutrient pool size achieved with functional microbial diversity (Fig. 2) alters these thresholds and shifts the sign of PSF under each combination of  $f_L$  and  $f_N$  (see also Tables S2 and S3).

Consider a system of  $P_L$  with a high litter decomposability, which tends to cause a positive PSF. The high decomposability allows the invasion of  $M_R$  into a system with  $M_S$  (resulting in either coexistence with  $M_S$  or dominance of  $M_R$ ) (Fig. 2B), which in turn leads to a smaller nutrient pool size ( $N^*$ ) than that in a system with  $M_S$  alone (when  $0.33 < f_L < 0.82$ ; Fig. 2A). The suppression of



**Fig. 3.** Roles of microbial diversity in determining the sign of PSF. Dependence of the sign of PSF on litter decomposabilities  $f_L$  and  $f_N$  is shown in a system with  $P_L$  only (" $P_L$ -dominant community") (A) and  $P_N$  only (" $P_N$ -dominant community") (B), respectively. There are three distinct configurations for the microbial community: a system with  $M_R$  only ("w/  $M_R$  only"),  $M_S$  only ("w/  $M_S$  only"), and with microbial diversity ("w/ diversity"). The sign of PSF is positive ("Positive PSF", "Positive", "+", or "+") or negative ("Negative PSF" or "Negative"). In a system with microbial diversity, the realized microbial composition depending on litter decomposability is shown as "Shifts in microbial composition" ( $M_S$ ,  $M_R$  and  $M_S$ , or  $M_R$ ). If the litter decomposability is too low, the system cannot persist ("no persistence"). Parameters are set to default values (Table S1).



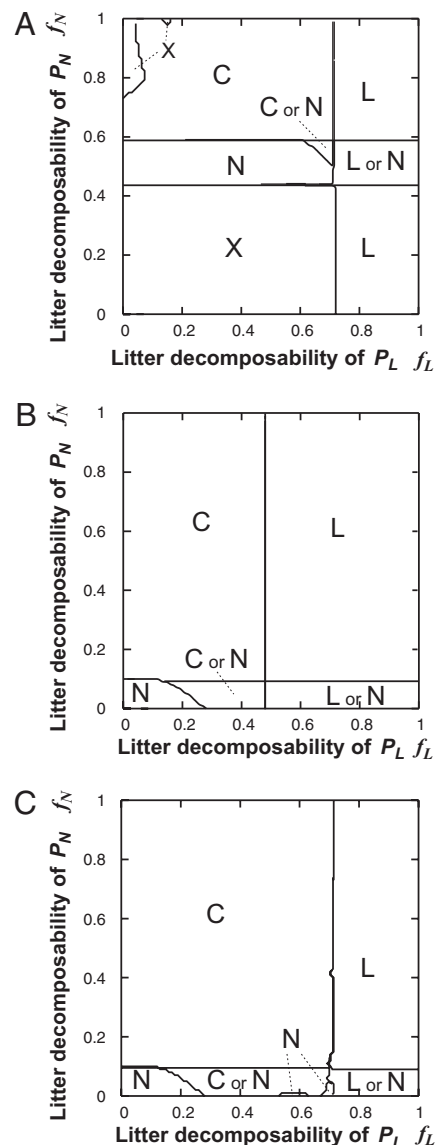
$N^*$  can shift the sign of PSF from positive to negative and increase the range of litter decomposabilities that cause a negative PSF (shaded ranges in Fig. 3A). Similarly, when  $P_N$  has a low litter decomposability and thus tends to cause a positive PSF, the invasion of  $M_S$  into a system with  $M_R$  increases the nutrient pool size (when  $f_L < 0.66$ ; Fig. 2A) and causes a negative PSF (shaded range in Fig. 3B). Microbial diversity may shift the sign of PSF from negative to positive, decreasing the range of litter decomposabilities that cause a negative PSF (Fig. S2 B and C). Nevertheless, such a facilitation of microbial diversity on negative PSF is observed in a wide range of parameter values (Figs. S3 and S4), indicating that microbial diversity tends to facilitate negative PSF.

**Roles of Microbial Diversity in Structuring the Plant Community.** The microbial diversity that facilitates negative PSF tends to promote the coexistence of plant species. This is confirmed by comparing the dependence of plant coexistence on plant litter decomposability ( $0 \leq f_L, f_N \leq 1$ ) in systems with a single microbial group ( $D_R$ -preferring microbes, Fig. 4A;  $D_S$ -preferring microbes, Fig. 4B) and in those with microbial functional diversity (Fig. 4C). Microbial functional diversity broadens the region where the two plant species can coexist (region C in Fig. 4C) compared with systems with a single microbial group (region C in Fig. 4A or B) (see also Fig. S5 for temporal dynamics and Fig. S6 for the realized microbial community composition). Microbial diversity also narrows the region where both plant species cause a positive PSF and either plant species can dominate depending on the initial abundance (region L or N in Fig. 4C). However, microbial diversity may not facilitate plant coexistence. For example, when the microbial assimilation efficiency ( $e_M$ ) is too high or too low, the region where the two plant species can coexist in a system with microbial diversity can be the same as that in a system with only  $M_R$  or  $M_S$  (Fig. S6 A and E, respectively). Yet even in such cases, microbial diversity never makes the plant coexistence region narrower than that in a system with only  $M_R$  or only  $M_S$  (Fig. S4).

## Discussion

**Effects of Microbial Diversity on Plant Litter Control over Nutrient Cycling.** The present study is a theoretical attempt to understand the role of microbial diversity in PSF functioning. Microbial diversity with the functional complementarity in decomposing different types of plant litter weakens plant control over nutrient cycling. This is achieved by a change in the relative microbial abundance in response to plant litter decomposability. Increasing litter decomposability tends to decrease the relative abundance of microbes that favor slowly decomposable litter (Fig. 2B). This lowers the decomposition rate of, and thus enhances accumulation of, slowly decomposable litter (Fig. 2B), suppressing an increase in net mineralization rate. Thus, microbial diversity acts as a “buffer” against plant control over nutrient cycling and decouples the relationship between litter decomposability and nutrient pool size (Fig. 2A and C). Our study presents a theoretical support for the hypothesis that microbial community weakens plant control over nutrient cycling (3).

Earlier studies, focusing on differences in the immobilization efficiencies of microbes, often argued that shifts in microbial composition reinforce plant control over nutrient cycling. This is because high (or low) litter decomposability favors bacteria (or fungi) with low (or high) immobilization efficiency and may enhance (or reduce) nutrient release rate from microbial biomass (14, 27, 28). Given the opposite prediction of the earlier hypothesis, it would be important to investigate how the immobilization efficiency and functional complementarity interact to determine the role of microbial diversity in plant control over soil. However, our model predicted that microbial diversity acts as the buffer even in the presence of differences in the immobilization efficiencies of microbes (Fig. S24).



**Fig. 4.** Consequences of PMSF on plant communities, as a function of the plant litter decomposability ( $f_L$  and  $f_N$ ). (A and B) Microbial community consisting of  $M_R$  (A) or  $M_S$  (B) only. (C) Microbial community consisting of  $M_R$  and  $M_S$ , and their realized community compositions as determined by PMSF. A better competitor for light ( $P_L$ ) is dominant in the plant community in region L, a better competitor for nutrient ( $P_N$ ) is dominant in region N, and the two plant species coexist in the region C. In region X, the ecosystem cannot persist because the plant litter decomposability of the dominant species or that of the invasional species is too low (see *S1 Text*, Section 5). Coexistence or dominance of  $P_N$  is realized in region C or N, and dominance of  $P_L$  or  $P_N$  is realized in region L or N, depending on the initial conditions. In a system with functional microbial diversity, dependence of the realized microbial composition (dominance of  $D_R$ - or  $D_S$ -preferring microbes or coexistence) on litter decomposability is not shown (Fig. S6). Although plant coexistence is realized by periodic succession with some combinations of litter decomposability, we did not distinguish this from coexistence at steady state. The presence of periodic succession may result in complex boundaries between region C or N, region N, and region L or N (see *S1 Text*, Section 5). Parameters are set to default values (Table S1).

The decoupling of the litter decomposability and nutrient pool size predicted here can arise also from the phenotypic plasticity of the immobilization efficiency in response to changes in litter quality (18) and the buffering effect of soil arthropods that can modify microbial activities and compositions (33). These previous hypotheses and the plant litter control hypothesis can be

tested against our hypothesis by manipulating the microbial community composition. The regression slope of the net mineralization rate or nutrient pool size with specific litter chemical traits (litter decomposability, e.g., C/N ratio, lignin concentration) will be smaller with increasing microbial diversity (our hypothesis), depend on the physiological flexibility of microbes (18) or the presence/absence/composition of soil arthropods (33), or be insensitive to these factors (plant litter control hypothesis).

**Microbial Diversity, Negative Feedbacks, and Plant Coexistence.** Plant diversity is essential for maintaining ecosystem productivity (34). If litter-mediated plant control over soils causes a positive PSF, it may hinder plant coexistence and then negatively affect ecosystem productivity. However, it has been proposed that interactions between plants and other trophic levels (e.g., herbivores and microbes) can change the plant control over soil and may contribute to the maintenance of plant diversity (3). Recent studies have suggested that mutualistic and parasitic microbes in the rhizosphere cause negative PMSF and facilitate plant coexistence (10–15). In contrast, the diversity of free-living microbial decomposers is thought to facilitate plant coexistence by moderately enhancing nutrient recycling and plant community productivity, or by providing a diverse range of plant-available soil resources, thus contributing to niche differentiation (14, 35, 36). However, these previous studies did not explicitly consider the impact of the plant community on the community composition of microbial decomposers and thus PMSF. Our model presents a mechanism for plant coexistence through feedbacks between the plant, free-living microbial decomposers, and the soil. Microbial diversity provides the microbial community with a functional flexibility, which buffers litter-mediated plant control over nutrient cycling (Fig. 2). This buffering effect prevents the realization of an extremely large or small nutrient pool size (Fig. 2) and a positive PSF (Fig. 3). On the contrary, it leads to intermediate levels of nutrient pool size ( $N_N^{**} < N^* < N_L^{**}$ ), which cause a negative PSF (Fig. 3) and facilitate the coexistence of plants (Fig. 4).

Although much more difficult to detect than PMSF systems caused by symbiotic microbes in the rhizosphere over short timescales, litter-mediated PMSF systems are important determinants for the plant community over long timescales. This is particularly true in stable and closed environments where plant litter is a major nutrient source and can locally control the nutrient pool size and plant community dynamics. Although not considered in this study, microbial diversity in open environments may affect the PSF by altering the nutrient exchange rates between systems. This issue is an open one for future studies.

The classic plant-centered view of nutrient cycling may be totally changed by considering the community ecology of microbial decomposers and their functional diversity. An approach that incorporates functional diversities within plant and microbial communities into nutrient cycling can be readily applied to other ecosystems (e.g., freshwater lakes and marine ecosystems) and uncover the role of microbial diversity in structuring those ecosystems. Our study has an implication on the effect of biodiversity on ecosystem resilience (37). The presence of positive feedbacks and multiple attractors in ecosystems can cause a discontinuous shift of ecosystem states in response to small environmental changes (37). We suggest that functional diversity within a trophic level may buffer the effects of another trophic level on ecosystem processes and prevent positive feedbacks, which would contribute to high ecosystem resilience (37).

## Methods

A multispecies patch occupancy model (38, 39) represents temporal changes due to interpatch recruitment and within-patch mortality in the proportion of patches occupied by  $P_L$  or  $P_N$ . The dynamics of  $P_L$  and  $P_N$  are represented by Eqs. 1 and 2, as follows:

$$dP_L/dt = r_L NP_L(1 - P_L - P_N) - m_P P_L + r_L NP_L P_N \quad [1]$$

$$dP_N/dt = r_N NP_N(1 - P_L - P_N) - m_P P_N - r_L NP_L P_N \quad [2]$$

The first term of Eqs. 1 and 2 represents new recruitment in empty patches (increasing with the inorganic nutrient level), the second term represents loss through a constant mortality rate ( $m_P$ ), and the last term represents the recruitment or loss resulting from individual-level competition (8). Although an individual of  $P_L$  has the advantage in within-patch local competition for light and can replace the individual of  $P_N$  that already occupies the patch,  $P_N$  has the higher colonization ability into an empty patch (higher reproductive ability and/or higher seedling survival rate) than  $P_L$  ( $r_N > r_L$ ). Plant individuals of species  $i$  take up a nutrient ( $b_i$ ) from the nutrient pool ( $N$ ) during each recruitment (primary production) and release it into the litter pool during each mortality (litter production). An individual plant may take up and release nutrients continuously after its establishment and until its death, at a rate of  $a_i N$  (annual primary production and litter production). The default setting for parameters assumes that  $b_L = b_N > 0$  and  $a_L = a_N = 0$ . Results with a positive value of  $a_i$  and species-specific values of biomass production ( $b_i$  and  $a_i$ ) (40) are shown in Figs. S3 and S4.

The litter pool consists of readily and slowly decomposable organic nutrients, with biomasses (nutrient contents)  $D_R$  and  $D_S$ , respectively. Readily decomposable  $D_R$  occupies the fraction  $f_L$  of the litter from plant  $P_i$  ( $i = L$  or  $N$ ).  $D_j$  ( $j = R$  or  $S$ ) is decomposed by two functional groups of soil microbes,  $D_R$ - and  $D_S$ -preferring microbes with biomasses  $M_R$  and  $M_S$ , respectively, at a rate of  $c_D(k_{jR}M_R + k_{jS}M_S)D_j$ . Here  $c_D$  represents the decomposition coefficient that is determined by external factors such as temperature. The dynamics of  $D_R$  and  $D_L$  are represented by:

$$dD_R/dt = f_L(b_L m_P + a_L N)P_L + f_N(b_N m_P + b_N r_L NP_L + a_N N)P_N - c_D(k_{RR}M_R + k_{RS}M_S)D_R \quad [3]$$

$$dD_S/dt = (1 - f_L)(b_L m_P + a_L N)P_L + (1 - f_N)(b_N m_P + b_N r_L NP_L + a_N N)P_N - c_D(k_{SR}M_R + k_{SS}M_S)D_S \quad [4]$$

where the first and second terms of Eqs. 3 and 4 represent the supply from  $P_L$  and  $P_N$ , respectively, and the third term is the loss through microbe-mediated decomposition (i.e., gross mineralization).

Because of differences in the chemical characteristics of the organic nutrients (e.g., carbon/nutrient ratio) and in the levels of secondary metabolites (e.g., tannins and phenolics), structural carbohydrates (lignin), and nutrient partitioning (e.g., nitrogen between photosynthetic enzymes and cell walls) (2, 41), the decomposition efficiency for  $D_R$  is higher than that for  $D_S$ , regardless of the microbial group (i.e.,  $k_{RR} > k_{SR}$  and  $k_{RS} > k_{SS}$ ). We assume a functional complementarity between two microbial functional groups for the decomposition of the two organic nutrient types, following that  $k_{RR} > k_{RS} > k_{SS} > k_{SR}$ . We can normalize  $k_{RR}$  as 1.0 without loss of generality, because the realized decomposition rate is weighted by  $c_D$ .

By separating decomposition, microbial growth (nutrient immobilization), and net mineralization, the following equations are derived for the dynamics of the microbial biomass ( $M_j$ ) and the inorganic nutrient ( $N$ ):

$$dM_j/dt = e_{Mj}c_D(k_{Rj}D_R + k_{Sj}D_S)M_j - m_{Mj}M_j \quad j = R \text{ and } S \quad [5]$$

$$dN/dt = -b_L r_L NP_L(1 - P_L) - b_N r_N NP_N(1 - P_L - P_N) - a_L NP_L - a_N NP_N + (1 - e_{MR})c_D(k_{RR}D_R + k_{SR}D_S)M_R + (1 - e_{MS})c_D(k_{RS}D_R + k_{SS}D_S)M_S + m_{MR}M_R + m_{MS}M_S \quad [6]$$

where the first through fourth terms of Eq. 6 represent the loss through plant uptake, and the other terms represent supply through the microbial pool (i.e., net mineralization process). The difference in the assimilation efficiency between two organic nutrients is not considered, with the assumption that microbial activity is strongly limited by nutrients and that nutrients in detritus are efficiently and maximally assimilated regardless of detritus quality. In other words, we did not consider the physiological flexibility in response to litter quality. We also did not consider complex for-

mation between nutrient and soil minerals, because our target nutrient is nitrogen rather than phosphorus.

The ecosystem is closed, such that the total amount of nutrients ( $T_N$ ) is constant over time (i.e.,  $b_L P_L + b_N P_N + D_R + D_S + M_R + M_S + N = \text{const} \equiv T_N$ ). This allows us to focus on the effects that the plant and microbe community dynamics have on the nutrient cycling rate and distribution of nutrients (i.e., living plant, litter, microbial biomass, and inorganic nutrient) in the system. We can set  $T_N$  as 1.0 without loss of generality. When either plant covers all patches,  $b_L$  or  $b_N$  ( $< T_N$ ) is allocated to the living plant biomass within the model ecosystem. We also assume that the microbial turnover rate (mor-

tality rate) is much larger than the plant turnover rate (i.e.,  $m_{Mj} > m_p$ ). Major nutrient fluxes in our model are shown in Fig. 1.

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