

LETTER

Plant and soil biodiversity have non-substitutable stabilising effects on biomass production

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Abstract

The stability of plant biomass production in the face of environmental change is fundamental for maintaining terrestrial ecosystem functioning, as plant biomass is the ultimate source of energy for nearly all life forms. However, most studies have focused on the stabilising effect of plant diversity, neglecting the effect of soil biodiversity, the largest reservoir of biodiversity on Earth. Here we investigated the effects of plant and soil biodiversity on the temporal stability of biomass production under varying simulated precipitation in grassland microcosms. Soil biodiversity loss reduced temporal stability by suppressing asynchronous responses of plant functional groups. Greater plant diversity, especially in terms of functional diversity, promoted temporal stability, but this effect was independent of soil biodiversity loss. Moreover, multitrophic biodiversity, plant and soil biodiversity combined, was positively associated with temporal stability. Our study highlights the importance of maintaining both plant and soil biodiversity for sustainable biomass production.

KEYWORDS

biodiversity loss, community-weighted mean, drought, dilution-to-extinction approach, ecosystem stability, functional diversity, multitrophic biodiversity, species asynchrony, temporal stability

INTRODUCTION

Understanding the mechanisms that stabilise ecosystem functions when faced with a changing environment has been a key issue in ecology (Craven et al., 2018; de Mazancourt et al., 2013; Hautier et al., 2014; Hector et al., 2010; Isbell et al., 2009; Loreau & de Mazancourt, 2013; Tilman & Downing, 1994; Tilman et al., 2006). Greater biodiversity, especially plant diversity, usually increases the temporal stability of biomass production, although negative and neutral effects have been occasionally observed (Craven et al., 2018; Hautier et al., 2014; Hector et al., 2010; Pennekamp et al., 2018; Tilman et al., 2006). However, the vast majority of existing studies focused on

the biodiversity of a single trophic group (Hautier et al., 2014; Hautier et al., 2015; Hector et al., 2010; Isbell et al., 2009; Ma et al., 2017; Tilman et al., 2006), neglecting biodiversity across trophic levels, even though multitrophic biodiversity has been shown to drive multiple ecosystem functions (Geisen et al., 2019; Schuldt et al., 2018; Soliveres et al., 2016).

Soil biota, comprising an enormous number of consumers and decomposers, represent one of the largest reservoirs of biodiversity on Earth (Geisen et al., 2019; Orgiazzi et al., 2016; Thakur et al., 2020). A growing number of studies suggest that soil biodiversity has an essential impact on plant diversity, community composition, biomass production, plant–plant interactions

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and plant tolerance to stress factors, as well as nutrient cycling (Bardgett & van der Putten, 2014; Delgado-Baquerizo et al., 2016; Domeignoz-Horta et al., 2020; Guerra et al., 2020; Liang et al., 2019; Wagg et al., 2014; Wagg et al., 2019). Recent work has provided a conceptual framework showing that plant and soil biodiversity can jointly influence the stability of biomass production via regulating these plant attributes (Yang et al., 2018). However, there is increasing concern that soil and plant biodiversity is threatened by anthropogenic environmental change (Banerjee et al., 2019; Geisen et al., 2019; Gossner et al., 2016; Tsiafouli et al., 2015; Zhou et al., 2020). Hence, it is important to understand how biodiversity loss in both soil and plant communities affects the stability of biomass production will provide a broader perspective.

Here we conducted a fully factorial experiment manipulating plant diversity and soil biodiversity using model grassland microcosms (Figure 1). We used a dilution-to-extinction approach (Hol et al., 2015; Roger et al., 2016; Wertz et al., 2006; Wertz et al., 2007; Yan et al., 2015) to create a gradient of soil biodiversity, and then established grassland microcosms of different plant species richness at each point along the soil biodiversity gradient under greenhouse conditions. We focused on the temporal stability of biomass production, defined as the ratio of the temporal mean

to the standard deviation of plant community biomass (Tilman et al., 2006). Because the constant environment in the greenhouse does not capture natural variability, environmental variation in precipitation was simulated by inducing three wet-dry cycles in all microcosms to investigate the effects of the biodiversity treatments on the temporal stability of biomass production.

Considering the significance of soil biodiversity for plant diversity, biomass production and plant–plant interactions (van der Heijden et al., 2008; Liang et al., 2019; Prudent et al., 2020; Wagg et al., 2014; Yang et al., 2018), we predicted that soil biodiversity loss will reduce the temporal stability of biomass production. Specifically, we tested whether and how soil biodiversity interacts with plant diversity in terms of species richness and functional diversity to influence temporal stability through their effects on plant–plant interactions and the temporal mean and the standard deviation of community biomass production. Furthermore, we investigated how multitrophic biodiversity, accounting for plant and soil biodiversity, affects temporal stability. We find that both greater plant and soil biodiversity had positive effects on the temporal stability of community biomass production, but plant and soil biodiversity independently affected temporal stability. In addition, multitrophic biodiversity is positively associated with temporal stability.

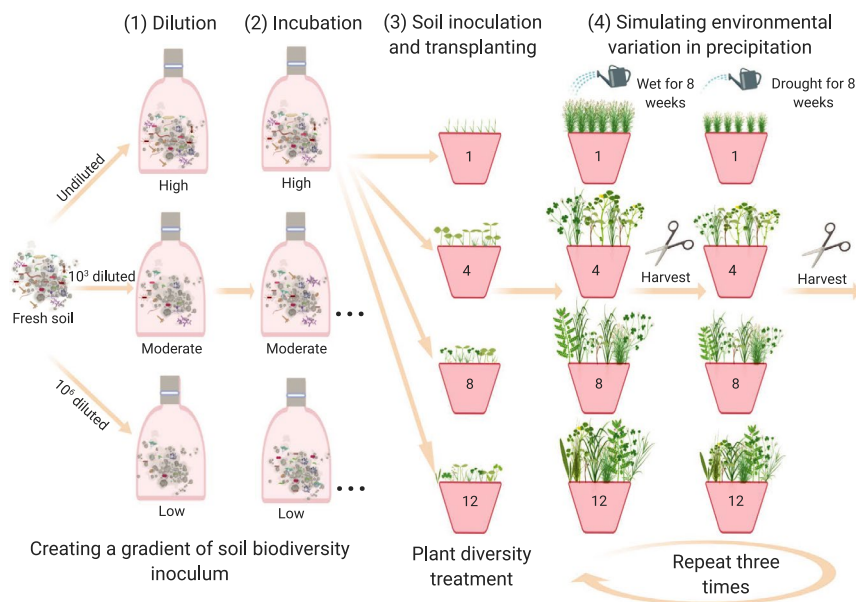


FIGURE 1 Scheme of the experimental design. (1) **Dilution.** Fresh field soil was kept undiluted or diluted 1×10^3 and 1×10^6 times using sterilised soil to create high, moderate and low soil biodiversity inocula respectively. (2) **Incubation.** Each soil bag was sealed using a sterilised cotton plug to avoid aerial microbial contamination while permitting gas exchange, and then incubated at room temperature in the dark until similar microbial biomass was observed among dilution treatments using the substrate-induced respiration method. (3) **Soil inoculation and transplanting.** After incubation, 200 g of soil inoculum was homogenised with 6800 g of sterilised soil and sand mixture (1:1) in each microcosm. Each microcosm received 24 seedlings from 1, 4, 8 or 12 plant species depending on plant diversity treatment. (4) **Simulating environmental variation in precipitation.** Three wet-dry cycles were implemented by maintaining gravimetric soil moisture of 12%–18% during the wetting periods and by watering until most plants started to wilt during the drying periods. At the end of each period, plant shoots were cut at 5 cm above the soil surface to determine shoot biomass production

MATERIAL AND METHODS

Experimental design

This experiment was set up as a fully factorial design containing all combinations of three levels of soil biodiversity (low, moderate, high) and four levels of plant species richness (1, 4, 8, 12 species) (Figure 1, Table S1 and the Supplementary Methods in the Supporting Information). The species pool contained 12 typical species from a local grassland in Brandenburg, Germany: four grasses (*Holcus lanatus*, *Anthoxanthum odoratum*, *Lolium perenne* and *Festuca rubra*), four herbs (*Daucus carota*, *Achillea millefolium*, *Hieracium pilosella* and *Plantago lanceolata*) and four legumes (*Trifolium repens*, *Vicia cracca*, *Medicago lupulina* and *Lotus corniculatus*). For single plant species treatment, each of 12 species was planted as a monoculture once at the moderate soil biodiversity treatment (12 microcosms) and twice at the low and high soil biodiversity treatments (24 and 24 respectively). We created the four- and eight-plant species treatments, which were replicated seven times, by randomly selecting plant species from the 12-species pool for each replicate at each soil biodiversity treatment (2 plant species levels \times 7 replicates \times 3 soil biodiversity levels = 42). The 12 species treatment contained all plant species, since there is only one way to combine 12 species from a pool of 12, and was replicated seven times at each soil biodiversity treatment (7 replicates \times 3 soil biodiversity levels = 21). For each replicate of plant diversity treatments, there was identical species composition among low, moderate and high soil biodiversity treatments to avoid a confounding effect of plant community composition and soil biodiversity treatments. In total, there were 12 treatments (4 plant species richness levels \times 3 soil biodiversity levels) and 123 grassland microcosms (12 + 24 + 24 + 42 + 21).

Soil inoculum preparation

We used the dilution-to-extinction approach (Domeignoz-Horta et al., 2020; Hol et al., 2015; Maron et al., 2018; Roger et al., 2016; Wertz et al., 2006; Wertz et al., 2007; Yan et al., 2015) to create high, moderate and low soil biodiversity (Figure 1). The fresh field soil, collected from the top 20 cm of the local grassland in Brandenburg (Rillig et al., 2010), was treated as the undiluted treatment. We diluted fresh soil with sterilised soil (autoclaving for 90 min at 121°C) to obtain the 10^{-3} and 10^{-6} dilutions (See the Supplementary Methods in the Supporting Information). To recover soil microbial biomass after dilution, all soil dilutions were incubated in a dark room (20°C) for 2 months, until no differences among soil dilutions were observed using the substrate-induced respiration method. The undiluted, 10^{-3} and 10^{-6} dilutions of soil inocula were treated as high,

moderate and low soil biodiversity treatments respectively. We stored 50 g of soil inoculum from each bag at -80°C for DNA extraction to determine the effectiveness of the dilution-to-extinction approach on soil microbial diversity.

Microcosms establishment and sampling

Soil and sand were mixed at a ratio of 1:1 and sterilised by autoclaving for 90 min at 121°C to remove plant seeds and soil biota. Each grassland microcosm (22.5 cm diameter and 16.5 cm height) was filled with 5.5 L (6.8 kg) of a sterilised soil and sand mixture. To reconstruct soil microbial communities with high, moderate and low soil biodiversity, 200 g of high, moderate or low soil biodiversity inoculum was carefully homogenised with the sterilised soil and sand mixture in each microcosm. After inoculation, microcosms with 1, 4, 8 and 12 plant species richness received 24, 6, 3 and 2 seedlings of each species, respectively, within 1 week. All microcosms were maintained in a climate-controlled greenhouse.

We simulated environmental variation in precipitation by inducing three wet-dry cycles (Figure 1). Each microcosm received deionised water twice weekly and water content was balanced biweekly by weight to maintain 60% of water holding capacity during the wet periods. During the dry periods, each microcosm received a maximum of 300 mL of deionised water only when most legumes and herbs started to wilt, and water content in each microcosm was balanced by weight to maintain 30% of water holding capacity. Each wet and dry period lasted at least for 8 weeks. At the end of each period, all plant shoots were harvested by cutting at 5 cm above the soil surface, sorted by species, oven-dried for 48 h at 70°C and weighed. In total, there were six such harvests, including shoot biomass from 17,712 plant individuals. Based on the maximum nutrients removed by the first harvest, 400 mL of Hoagland nutrient solution was added to each microcosm after each harvest.

Soil fungal and bacterial diversity

After the final harvest, 100 g of fresh soil was collected from each of the 12-species microcosms in each soil biodiversity treatment and stored at -80°C for DNA extraction to evaluate the recolonisation of soil microbes during the experimental period. There was identical plant community composition among the 12-species microcosms, minimising the confounding effect of plant community composition on soil microbes. DNA from each soil inocula and fresh soil samples of the final harvest was extracted from 250 mg soil, using DNeasy PowerMax Soil Kits (MoBio Laboratories Inc.), following the manufacturer's instructions. Soil fungal and bacterial diversity were determined following Illumina

MiSeq high-throughput sequencing with ITS7 and ITS4 for fungi and 515f and 806r for bacteria (Fierer et al., 2005; Ihrmark et al., 2012). Sequencing raw data were processed using DADA2 (Callahan et al., 2016) to obtain denoised, chimera-free, non-singleton amplicon sequence variants (ASVs). We used soil fungal and bacterial diversity together, indicated by the sum of bacterial and fungal ASVs, to indicate soil biodiversity hereafter. Details of soil biodiversity determinants can be found in the Supporting Information.

Measures of stability indices

The temporal stability of plant community biomass production in each microcosm is defined as μ/σ , where μ is the temporal mean of biomass production during three rounds of wet–dry cycles, and σ is the standard deviation of biomass production across this experimental period (Tilman et al., 2006). We partitioned the temporal stability into community-wide plant species asynchrony and weighted population variance (Thibaut & Connolly, 2013). Plant species asynchrony (Loreau & de Mazancourt, 2008) was calculated as $1 - \varphi = 1 - \sigma^2 / (\sum_{i=1}^s \sigma_i^2)$, where φ is species synchrony, σ^2 the temporal variance of biomass production, σ_i is the standard deviation in the shoot biomass of species i in a community with S species. If $1 - \varphi$ equals 0, species fluctuate synchronously, indicating that there is no compensatory effect; if $1 - \varphi$ is higher than 0, species fluctuate asynchronously, indicating that there are compensatory effects (Loreau & de Mazancourt, 2008; Song & Yu, 2015). Asynchrony of plant functional groups was calculated by replacing species i by each plant functional group, which indicates the strength of asynchronous responses at the plant functional group level. Weighted population variance (CV_{pop}) is defined as $CV_{pop} = (\sum_{i=1}^s \sigma_i) / \mu$. A decrease in population variance can promote temporal stability by reducing the variability of populations (Thibaut & Connolly, 2013).

Functional composition and diversity

To better understand the role of plant diversity, we calculated four functional diversity indices for plant communities in each microcosm using 10 leaf and root traits relevant to drought tolerance: functional richness, functional evenness, functional divergence and functional dispersion (Fischer et al., 2016; Freschet et al., 2021; Laliberté & Legendre, 2010; Liu et al., 2018; Lozano et al., 2020; Mahaut et al., 2020; Villéger et al., 2008) (See the Supplementary Methods for details). These data were obtained from a previous study (Lozano et al., 2020), conducted in the same greenhouse as this study. Principal component analysis (PCA) of community-weighted means of ten traits was employed, using the

PCA function in *FactoMineR* (Lê et al., 2008). The first axis of PCA analysis was treated as an index of the community-weighted mean (CWM) of all traits (Craven et al., 2018; Mahaut et al., 2020). Functional diversity indices of each harvest were calculated and then were averaged across the six harvest time points.

Statistical analysis

We used linear models to test the effects of the dilution-to-extinction approach on soil microbial, fungal and bacterial diversity and respiration rates. Microbial data were log-transformed before analyses to meet the normality assumption. We also used a linear model to test whether soil biodiversity interacts with plant diversity to influence response variables. Plant species richness was log-transformed to represent the biodiversity effect which typically saturates with increasing species richness due to increasing redundancy (Hautier et al., 2014). For each response variable, a weighted least squares regression was applied to take heteroscedasticity into account. Since variance differed with plant species richness, each sample was weighted with an inverse of the variance at each plant species richness level. We evaluated the importance of the interaction between soil biodiversity and plant diversity treatments based on model comparison using the Akaike information criterion (AIC) that compares the additive model (soil biodiversity + plant species richness) and the interactive model (the additive model with their interaction term).

The initial plant species richness and the total number of fungal and bacterial ASVs in the soil inoculum were standardised by scaling them to the maximum values at the beginning of this study. Then, we calculated multitrophic biodiversity as an average of the standardised plant species richness and the number of soil microbial ASVs (Allan et al., 2014), to investigate the effect of multitrophic biodiversity on stability-related indices. Compared with polynomial, quadratic and exponential models in regression analysis, linear models fitted the data better and were employed to test the relationships between multitrophic biodiversity and stability-related indices.

We tested whether soil biodiversity affects the interactions among plant functional groups by comparing responses of plant functional groups in the monocultures and species-mixed communities. In the monocultures, a mixed-effect model with harvest time point and plant species as random factors was employed to investigate the effect of soil biodiversity loss on shoot biomass of individual plant functional group. By excluding monocultures, we further tested the effect of soil biodiversity and plant species richness on shoot biomass of plant functional groups using a mixed-effect model with harvest time point as a random factor. These analyses were conducted by sub-setting data of wet and dry periods, separately. All

data analyses were performed in the software *R* 4.0.4 (R Core Team, 2021). For data handling, analysis and visualisation, we used the packages *dplyr*, *tidyr*, *vegan*, *FD*, *MASS*, *nlme*, *FactoMineR*, *ggplot2*, *patchwork*, *ggridges*, *reshape2*, *AICcmodavg* and *cowplot*. Details of data analysis can be found in the Supporting Information and *R* code. [Correction added on 8 June 2021, after first online publication: the word gegen has been corrected to vegan.]

RESULTS

Soil microbial diversity

The dilution-to-extinction approach was successful in creating a gradient of soil microbial (bacterial and fungal) diversity; importantly, soil microbial biomass, as indicated by respiration rates, was recovered after incubation (Figure 2A, B and C; Table S2). Compared with the undiluted soil inocula, 57.91% of soil microbial taxa was lost through the 10^{-3} dilution, and 78.18% was lost during the following 10^{-6} dilution based on the number of soil microbial amplicon sequence variants (ASVs) (Figure 2A). Low-abundance taxa, for instance, *Chytridiomycota* and *Acidobacteria*, were first eliminated during dilution (Figure 2B and C). Although microcosms were open to microbial re-colonisation from the air and water, which increased soil bacterial diversity especially in the low soil biodiversity treatment, differences of fungal diversity were still observed among soil dilution treatments at the end of the experiment (Figure S1 and Table S2). Besides, the diversity of fungal mutualists in the phylum of *Glomeromycota* was dramatically decreased at the 10^{-3} dilution and fungal mutualists were absent at the 10^{-6} dilution at the end of the experiment (Figure S1A and Table S2). The diversity of plant fungal pathogens was decreased by soil dilution in the soil inocula, and was not altered at the last harvest (Table S2).

Temporal stability of plant community biomass production

Model selection with the Akaike information criterion (AIC) suggests that the additive models including soil and plant diversity were better than the corresponding models with the interaction term to explain all aspects of temporal stability (i.e. temporal stability, mean, standard deviation, asynchrony and population variance) (Table S3 and S4). This indicates that soil biodiversity and plant diversity independently influenced stability-related indices (Figure 3; Table S5 and S6). Soil biodiversity loss had consistent negative effects on the temporal stability of community biomass production and plant species asynchrony along a gradient of plant species richness, and plant species richness was positively associated with the temporal stability of community biomass production and plant species asynchrony (Figure 3A and B). Soil biodiversity and plant species richness did not affect population variance (Figure 3D). The temporal mean of community biomass production was positively related to plant species richness, whereas the standard deviation was negatively correlated with plant species richness (Figure 3C and E). Soil biodiversity loss did not alter the temporal mean of community biomass production, whereas statistically significantly increasing the standard deviation (Figure 3C and E). Asynchrony at both plant species and functional group level was positively related to the temporal stability of community biomass production, whereas soil biodiversity loss did not exert a significant effect on the asynchrony–stability relationship (Figure S2). When monocultures were excluded from the analysis, plant species richness did not exert a significant effect on the temporal stability of community biomass production, although the effect of soil biodiversity was still observed (Table S5).

However, functional diversity in terms of functional richness increased the temporal stability of plant

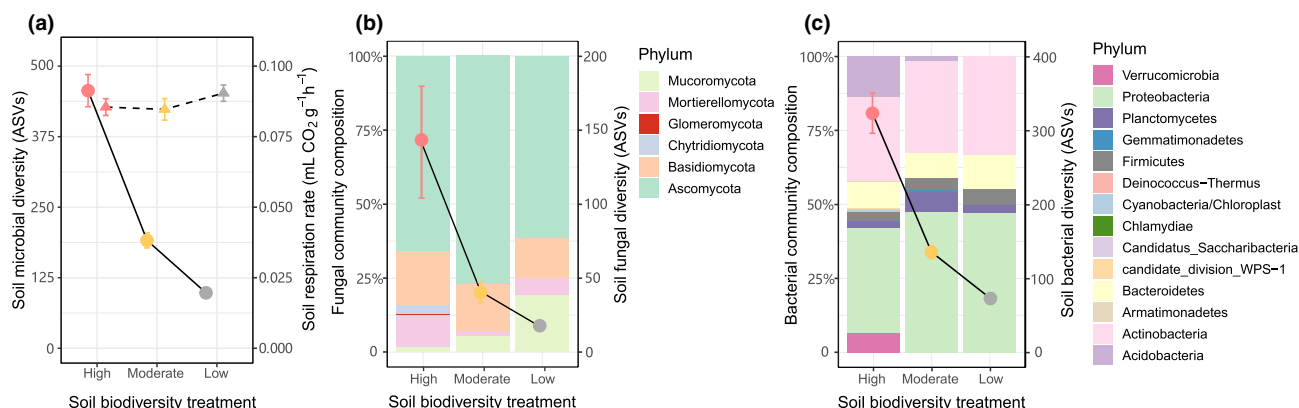


FIGURE 2 The effect of the dilution-to-extinction approach on microbial diversity, biomass (indicated by soil respiration rate after incubation) and community composition of the original soil inocula. (A) The dilution-to-extinction approach successfully reduced soil microbial diversity (solid line) but did not alter the soil respiration rate (dash line). The dilution-to-extinction approach dramatically reduced fungal (B) and bacterial (C) diversity and altered the community composition of soil microbes based on amplicon sequence variant (ASV) detection

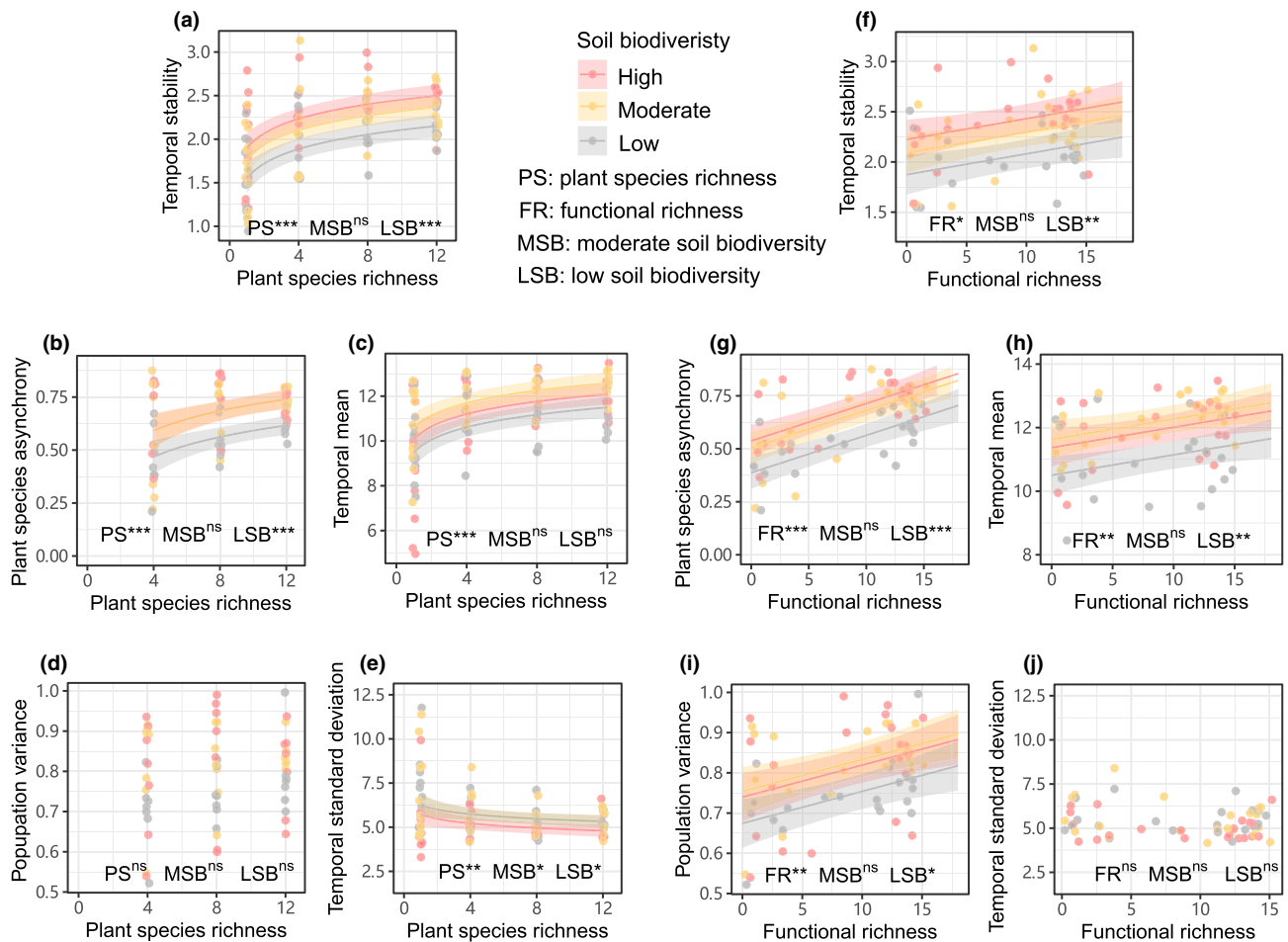


FIGURE 3 Plant and soil biodiversity independently influence stability-related indices. (A–E) The effects of plant species richness (PS) and soil biodiversity on the temporal stability, mean and standard deviation of community biomass production, and plant species asynchrony and population variance. (F–J) The effects of plant functional richness and soil biodiversity loss on these stability-related indices. The effects of treatments on temporal stability were partitioned into the effects on plant species asynchrony and population variance, or the effects on temporal mean and standard deviation of community biomass production. Light bands represent 95% confidence intervals. Note: moderate and low soil biodiversity effects refer to the differences to the high soil biodiversity treatment. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$

communities excluding monocultures (Figure 3F). Plant species asynchrony, population variance and the temporal mean of community biomass production were increased by functional richness, and were decreased by soil biodiversity loss (Figure 3G, H and I). Soil biodiversity loss and functional richness did not alter the standard deviation of community biomass production (Figure 3J). Furthermore, functional richness was closely related to plant species richness, and 78% of the variance was explained by an additive model, which was much higher than that of other functional diversity indices ($R^2 < 0.4$, Table S6). Plant species richness did not contribute to the functional evenness and the community-weighted mean of all traits (Table S6). Functional divergence and dispersion were increased by plant species richness (Table S6), but were not correlated with the temporal stability (Table S7).

Multitrophic biodiversity, calculated from plant and soil biodiversity, was positively associated with the temporal stability of community biomass production, plant

species asynchrony and the temporal mean of community biomass production, and negatively correlated with the standard deviation of community biomass production (Figure 4A, B, C and E). Multitrophic biodiversity was not related to population variance (Figure 4D). These linear relationships indicate that multitrophic biodiversity can drive the temporal stability of community biomass production through an increase in either soil biodiversity or plant species richness.

Plant community composition

Plant species loss and community evenness were affected by either soil biodiversity or plant species richness, but were not related to the temporal stability of community biomass production (Table S5). In the monocultures, soil biodiversity did not affect the temporal stability of grasses, whereas increasing the temporal stability of herbs and legumes (Figure S3A, B and C).

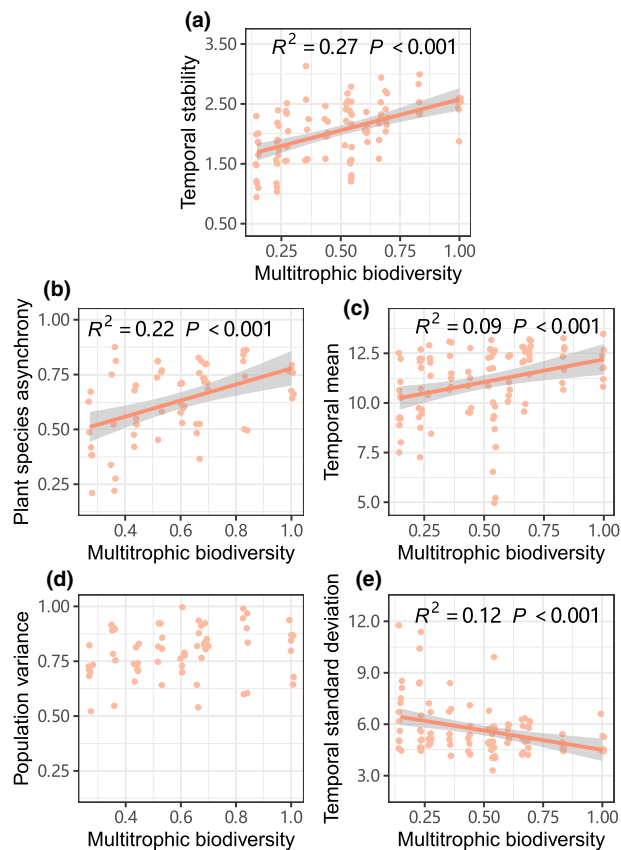


FIGURE 4 Relationships between multitrophic biodiversity and (A) the temporal stability of community biomass production, (B) plant species asynchrony, (D) population variance, (C) the temporal mean and (E) standard deviation of community biomass production. The effects of treatments on temporal stability were partitioned into the effects on plant species asynchrony and population variance, or the effects on temporal mean and standard deviation of community biomass production. Light bands represent 95% confidence intervals

In mixed-species communities, plant species richness increased the temporal stability of grasses, but did not affect the temporal stability of herbs and legumes (Figure S3D, E and F). Moderate soil biodiversity increased the temporal stability of herbs, whereas soil biodiversity did not influence the temporal stability of grasses and legumes in mixed-species communities (Figure S3D, E and F). Soil biodiversity loss increased the proportional abundance of grasses in mixed-species communities, but decreased the proportional abundance of herbs and legumes (Figure S3G, H and I). The proportional abundance of grasses was positively associated with the temporal stability of community biomass production, whereas the proportional abundance of herbs and legumes was negatively associated with temporal stability (Figure S3J, K and L). However, soil biodiversity loss still had negative effects on the temporal stability of community biomass production (Figure S3J, K and L).

Soil biodiversity loss did not alter the shoot biomass of grasses and herbs during wet and dry periods in the monocultures (Table S8 and Figure S4). Shoot biomass of legumes was increased by soil biodiversity loss during

wet periods, and was not altered during dry periods in the monocultures. In mixed-species communities, the effects of soil biodiversity loss on shoot biomass of plant functional groups were similar along a gradient of plant species richness (Table S8 and Figure S4). For instance the loss of soil biodiversity increased the growth of grasses, while strongly decreasing the growth of herbs and legumes, independently of plant species richness. On average, there was at least twice as much shoot biomass of grasses as legumes or herbs at low soil biodiversity. Plant species richness did not affect the shoot biomass of plant functional groups during wet periods, but tended to increase their shoot biomass during dry periods.

DISCUSSION

Our findings show that plant and soil biodiversity have non-substitutable impacts on the temporal stability of community biomass production. In this study, soil biodiversity loss had a detrimental effect on temporal stability by reducing the community-level mean biomass production, increasing the temporal variability and weakening compensatory effects (via facilitation of uneven community composition favoring grasses over herbs and legumes). Consistent with previous studies (Craven et al., 2018; Hautier et al., 2014; Hautier et al., 2015; Hector et al., 2010; Tilman et al., 2006), an increase in plant diversity in terms of both species richness and functional diversity promoted temporal stability. However, plant and soil biodiversity exerted independent influences on temporal stability. Furthermore, multitrophic biodiversity, calculated from plant and soil biodiversity, was positively and linearly associated with the temporal stability of community biomass production. A large number of studies suggest that the biodiversity of a single trophic group, e.g. the diversity of plants, is a major factor stabilising biomass production (Craven et al., 2018; Hautier et al., 2014; Hautier et al., 2015; Hector et al., 2010; Pennekamp et al., 2018; Tilman et al., 2006). Our study suggests that maintaining ecosystem functions (e.g. biomass production) when faced with environmental variability requires high soil biodiversity, in addition to plant diversity.

Compared with plant species richness, the diversity of plant functional traits was a better explanatory variable for temporal stability in diverse plant communities. Exploitative plant species with fast-growing acquisitive traits, e.g. high specific leaf area, leaf nitrogen concentration, specific root length and specific root surface area, could recover rapidly the following disturbance, whereas conservative species with slow-growing traits, e.g. low leaf dry matter concentration, high root average diameter and root tissue density, may have a higher resistance to disturbance (Fischer et al., 2016; Freschet et al., 2021; Liu et al., 2018; Lozano et al., 2020; Mahaut et al., 2020). Plant communities with a higher diversity of functional traits likely imply a stronger asynchronous

response of plant species, e.g. a decrease in exploitative plant species compensated by conservative species during a disturbance, and *vice versa*. In this study, the diversity of plant functional traits increased plant species asynchrony, and subsequently, promoted the temporal stability of biomass production.

Plant species asynchrony is a main underlying mechanism by which plant diversity stabilises biomass production when faced with disturbance (Craven et al., 2018; de Mazancourt et al., 2013; Hautier et al., 2014; Hector et al., 2010; Isbell et al., 2009; Loreau & de Mazancourt, 2008; Loreau & de Mazancourt, 2013; Thibaut & Connolly, 2013; Zhang et al., 2019). Supporting past studies, we found that higher plant species richness, soil biodiversity and multitrophic biodiversity promoted the temporal stability of biomass production via enhancing plant species asynchrony. A previous study found that the presence of natural soil biota dramatically increased the growth of legumes and herbs, and thus, promoted plant species asynchrony under simulated environmental variation in precipitation (Pellkofer et al., 2016). In addition to plant diversity, our results suggest that soil biodiversity is an alternative pathway of promoting the occurrence of asynchrony of plant species and particularly functional groups. In accordance with past research (Prudent et al., 2020; Wagg et al., 2014; Wagg et al., 2019; Yang et al., 2021), we found that soil biodiversity enhanced the performance of herbs and legumes during wet and dry periods, likely indicating higher resistance during dry periods or faster recovery during wet periods. Specifically, herbs had the opportunity to recover from drought and differed from grasses in response to the simulated variation in precipitation at high soil biodiversity (Fig. S4). Besides, the dramatic reduction in legumes was compensated by the rapid growth of grasses during the first drought disturbance at high and moderate soil biodiversity. However, the compensatory effect was weaker in low soil biodiversity because legumes had already been suppressed by soil biodiversity loss before the first drought disturbance. Several studies show that soil biodiversity is more important for herbs and legumes than grasses in plant communities, and especially for the persistence of legumes (Prudent et al., 2020; Wagg et al., 2014; Yang et al., 2021). This is probably because the growth of herbs and legumes is more reliable in the presence of specific soil biota, e.g. plant growth-promoting bacteria and mycorrhizal soil mutualists (van der Heijden et al., 2008; Hoeksema et al., 2010; Prudent et al., 2020; van der Heijden et al., 2016). The absence of these soil mutualists, in addition to the loss of soil biodiversity, could have suppressed the performance of herbs and legumes during and following drought in this study.

It should be noted that soil biodiversity loss did not affect the growth of herbs and grasses, and even increased the growth of legumes in the monocultures during wet conditions probably because of the reduction in plant

pathogens by soil dilution. Therefore, soil biodiversity influenced the performance of plant functional groups by regulating the interactions among functional groups in the mixed-species communities. For instance soil biodiversity increased the mean of plant community evenness by favouring herbs and legumes. Although biodiversity can enhance temporal stability by promoting community evenness (Thibaut & Connolly, 2013), we found that plant community evenness was not related to the temporal stability of community biomass production. Because the proportional abundance of grasses was positively related to temporal stability, soil biodiversity loss should increase temporal stability by promoting the dominance of grasses. However, soil biodiversity loss exerted a negative effect on temporal stability. Thus, the detrimental effect of soil biodiversity loss on temporal stability cannot be directly attributed to its effect on community evenness and the dominance of grasses, but can come from a decrease in asynchrony of plant functional groups.

A decrease in population variance can contribute to the temporal stability of biomass production, because the effects of treatments on temporal stability can be decomposed into their effects on plant species asynchrony and population variance (Thibaut & Connolly, 2013). The higher functional richness and soil biodiversity increased population variance, which should decrease temporal stability. However, these detrimental effects were neutralised by an increase in plant species asynchrony. Besides, an increase in the temporal stability of biomass production can also be caused by both, an increase in the temporal mean of biomass production and a reduction in the temporal standard deviation (Hautier et al., 2014; Tilman et al., 2006). Consistent with most earlier studies (Craven et al., 2016; Hautier et al., 2014; Tilman et al., 2014; Weisser et al., 2017), our study supports the hypothesis that an increase in plant species richness can promote biomass production and decrease the temporal standard deviation of biomass production.

Soil biodiversity loss can decrease or increase biomass production, which depends on soil biodiversity and soil community composition (Wagg et al., 2014). Our results suggest that the temporal mean of biomass production was not altered by soil biodiversity loss when monocultures were included, whereas the temporal mean was decreased when monocultures were excluded (Figure 3C and H). This suggests that soil biodiversity loss has a detrimental effect on the temporal mean of biomass production in diverse plant communities. However, soil biodiversity loss did not affect plant diversity–productivity relationships in diverse plant communities. Past research shows soil pathogen suppression has more beneficial effects, whereas the absence of soil mutualists exerts stronger detrimental effects on biomass production in less diverse plant communities, and consequently, influences plant diversity–productivity relationships (Klironomos et al., 2000; Liang et al., 2019; Luo et al., 2017; Maron

et al., 2011; Schnitzer et al., 2011; Wang et al., 2019). However, soil biodiversity loss did not alter the strength of plant diversity effects on plant biomass production in this study. These results indicate that the effect of soil biodiversity loss on plant productivity could not be simply due to the loss of single soil pathogens or mutualists. In this study, soil biodiversity loss reduced plant fungal pathogens in soil inocula, and reduced or even eliminated mycorrhizal soil mutualists in the phylum of *Glomeromycota* at the last harvest. Reductions in soil pathogens and mutualists have opposite effects on plant biomass production, and therefore, effects of reductions in soil pathogens and mutualists along soil biodiversity loss might cancel each other out. A decrease in plant productivity could be caused by soil biodiversity loss in general other than the loss of soil mutualists along with soil biodiversity loss (Prudent et al., 2020; Yang et al., 2021).

Our study sheds new light on the consequences of multitrophic biodiversity loss under global anthropogenic change. Anthropogenic influences have been shown to destabilise biomass production via reducing plant diversity (Hautier et al., 2015). Moreover, global anthropogenic change, such as nitrogen deposition, land-use intensification, warming, fertilisation and drought, can threaten both soil and plant biodiversity (Banerjee et al., 2019; Geisen et al., 2019; Gossner et al., 2016; Hautier et al., 2015; Rillig et al., 2019; Tsiafouli et al., 2015; Zhou et al., 2020). Our study suggests that the loss of multitrophic biodiversity could reduce the temporal stability of biomass production by suppressing the occurrence of plant species asynchrony or decreasing the mean of biomass production and increasing its variation. These results indicate that the prediction of biomass production under global anthropogenic change requires a multitrophic evaluation of biodiversity loss.

In this study, the dilution-to-extinction approach, which has been widely used to investigate the relationships between rare soil microbial species and ecosystem functions (Domeignoz-Horta et al., 2020; Hol et al., 2015; Maron et al., 2018; Roger et al., 2016; Wertz et al., 2006; Wertz et al., 2007; Yan et al., 2015), was employed to create a gradient of soil biodiversity. Our results confirm that less abundant taxa were lost first during dilution, followed by more abundant taxa (Maron et al., 2018; Roger et al., 2016; Yan et al., 2015). This approach can simulate a realistic loss of soil biodiversity (Maron et al., 2018; Roger et al., 2016; Wertz et al., 2006; Yan et al., 2015), because less abundant taxa have a higher risk of extinction than abundant species under anthropogenic changes (Zhou et al., 2020). This study used an open system, and an increase in bacterial phyla was observed, compared to the initial soil inoculum. This means that propagules from the environment contributed to soil biodiversity at the last harvest. Contamination in a sterile treatment was even detected in closed systems (Wagg

et al., 2014) and is generally difficult to avoid. Because soil biodiversity generally had a positive effect on ecosystem functions in previous studies and our present study, this indicates that we have underestimated the effect of soil biodiversity loss on the temporal stability of biomass production.

Besides, the temporal stability of biomass production was assessed by clipping shoot biomass following variation in watering regimes within a single season in this study. This prevented any plant community dynamics through differences in plant reproduction and recruitment from influencing stability indices. However, soil biodiversity loss may have more detrimental effects on stability indices in long-term field experiments, because soil microbes are of great importance for the regeneration of plant communities (van der Heijden et al., 2008; van der Putten, 2017; Yang et al., 2018). Additionally, the stabilising effect of plant diversity could be underestimated in a short-term experiment, as previous studies observed an increase in the plant diversity effect on plant–plant interactions and biomass production through time (Huang et al., 2018; Forest et al., 2018).

In summary, our study suggests that plant and soil biodiversity play non-substitutable roles in stabilising plant community biomass production. Although greater plant diversity can promote the temporal stability of biomass production, the reduction in temporal stability induced by soil biodiversity loss cannot be compensated via increasing plant diversity. This result highlights the significance of multitrophic biodiversity for stabilising ecosystem functions. Our study has important implications for restoration and conservation management in terrestrial ecosystems. First, it is important to preserve biodiversity at multiple trophic levels to stabilise ecosystem functions, especially in ecosystems suffering from intense disturbance. Second, although biomass production can be stabilised via increasing plant diversity by restoration or conservation measures, we should not ignore the importance of maintaining soil biodiversity, since low levels of soil biodiversity can destabilise biomass production.

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AUTHORS' CONTRIBUTIONS

GY and MCR conceived the ideas and designed the study. GY set up the experiment and collected the data, with important suggestions from SH. MR, JR and GY

analysed the data. GY, MR and JR wrote the first draft, and all authors commented on the manuscript.

PEER REVIEW

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OPEN RESEARCH BADGES



This article has earned Open Data badge. Data is available at <https://doi.org/10.6084/m9.figshare.14381321.v3>.

DATA AVAILABILITY STATEMENT

The data and R code are available via the figshare (<https://doi.org/10.6084/m9.figshare.14381321.v3>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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