

RESEARCH ARTICLE

Plant diversity and community age stabilize ecosystem multifunctionality

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Abstract

It is well known that biodiversity positively affects ecosystem functioning, leading to enhanced ecosystem stability. However, this knowledge is mainly based on analyses using single ecosystem functions, while studies focusing on the stability of ecosystem multifunctionality (EMF) are rare. Taking advantage of a long-term grassland biodiversity experiment, we studied the effect of plant diversity (1–60 species) on EMF over 5 years, its temporal stability, as well as multifunctional resistance and resilience to a 2-year drought event. Using split-plot treatments, we further tested whether a shared history of plants and soil influences the studied relationships. We calculated EMF based on functions related to plants and higher-trophic levels. Plant diversity enhanced EMF in all studied years, and this effect strengthened over the study period. Moreover, plant diversity increased the temporal stability of EMF and fostered resistance to reoccurring drought events. Old plant communities with shared plant and soil history showed a stronger plant diversity–multifunctionality relationship and higher temporal stability of EMF than younger communities without shared histories. Our results highlight the importance of old and biodiverse plant communities for EMF and its stability to extreme climate events in a world increasingly threatened by global change.

KEYWORDS

biodiversity, climate extremes, drought, ecosystem functioning, resilience, resistance, temporal stability

1 | INTRODUCTION

Numerous studies have demonstrated that an increase in biodiversity improves single ecosystem functions, such as plant productivity

(Cardinale et al., 2007; Guerrero-Ramírez et al., 2019; Hector et al., 1999; Marquard et al., 2009), but also the simultaneous performance of multiple functions, the so-called ecosystem multifunctionality (EMF; Fanin et al., 2018; Hautier et al., 2018; Schuldt

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et al., 2018). EMF reflects the complexity of ecosystems by aggregating (many) individual functions, that is, functions across multiple trophic levels above- and belowground (Manning et al., 2018). The positive relationship between biodiversity and EMF is mainly explained by the fact that a large number of species can provide a wide range of functions (Eisenhauer et al., 2018; Meyer et al., 2018). Single species may appear to be redundant on a small scale (e.g., over a short period of time) in terms of the functions they provide, but each species' functions are important at some point, either in different years, different places, or under different environmental conditions (Eisenhauer et al., 2023; Isbell et al., 2011), which may imply that biodiversity can be more important for multifunctionality than for single functions.

Despite this, EMF has been less intensively studied in BEF research compared to single functions. For example, many long-term biodiversity experiments have shown that the temporal stability of ecosystems (e.g., temporal variation, resistance, and resilience) increases with species richness as well as the age of the community (Isbell et al., 2015; Schnabel et al., 2021; Tilman et al., 2006; van Moorsel et al., 2021; Wagg et al., 2017, 2022). The underlying reason is that species-rich and old, established plant communities benefit more from complementarity effects and positive plant-soil interactions (Cardinale et al., 2007; Reich et al., 2012; Thakur et al., 2021), which make them more resistant against disturbances (Bennett et al., 2020; Craven et al., 2016; Wang et al., 2021) and thus more stable through time (Ren et al., 2022; Wagg et al., 2022; Yang et al., 2018). However, these findings are based mainly on analyses of single functions (in most cases, plant biomass production). This raises the question whether these results are indicative for “whole-ecosystem” responses to environmental perturbations. For instance, it is unclear if there are any trade-offs in the stability of different ecosystem functions, causing an overall neutral effect of biodiversity on the temporal stability of EMF (Argens et al., 2024). However, it is also possible that multifunctionality is inherently more stable than single functions, as the combination of many functions could create a portfolio effect (Doak et al., 1998; Tilman, 1999; Yachi & Loreau, 1999). Given these competing hypotheses, and due to the low number of studies in this field, there is an urgent need to fully understand the relationship between biodiversity and temporal stability of EMF (Jing et al., 2022; Sasaki et al., 2019).

To fill these critical knowledge gaps, we investigated the effect of plant diversity on EMF and its stability over 5 years (2017–2021) in a long-term grassland biodiversity experiment in Germany (the Jena Experiment; Weisser et al., 2017). To calculate multifunctionality, we used plant-related functions as well as above- and belowground functions not related to plants in order to represent a wide range of functions (nine functions in total). For plants, we used functions that provide information about plant community performance (aboveground productivity and cover), invasion stability (plant invasion resistance), habitat structure, space and shading (plant community height), and photosynthetic capacity (leaf area index, LAI; Garland et al., 2021). In addition, we used functions that are not directly related to plants, but are associated with higher-trophic levels and

abiotic ecosystem processes. For belowground functions, we considered microbial activity (microbial biomass carbon, microbial basal respiration), which provides information on decomposition rates, but also on top-down control of plants by microbial plant pathogens (Garland et al., 2021). Furthermore, we used soil moisture as an ecosystem function, as soil water availability is a critical ecosystem property that determines biological activity across trophic levels. In terms of aboveground functions, we used herbivory and predation, which provide information on top-down and pest control (Garland et al., 2021). With this selection, we included representatives of all types of ecosystem functions, namely regulatory, provisioning, and supporting functions (Garland et al., 2021). To exclude the possibility that plant-related functions are more strongly considered in the multifunctionality index than higher-trophic level functions (because plant-related functions are more interrelated), which could bias the results towards a plant-related response, we calculated and compared plant-related and higher-trophic level multifunctionality, in addition to total multifunctionality.

The study was conducted in plots of the so-called Δ BEF experiment (Vogel et al., 2019) with a gradient in plant species richness (1, 2, 4, 8, 16, 60 species) and split-plot treatments of shared plant or soil history (i.e., old vs. young). Old plant communities were already established in 2002 (i.e., 15 years), so plants and soil shared a common history, while new and re-sown plant communities were established in 2016. For new communities, the soil was removed, filled with fresh agricultural soil, and re-sown (i.e., no shared history), while for the re-sown communities, vegetation was removed, the soil was maintained, and new seeds were sown (i.e., shared soil history but without plant history). This design allowed us to test how plant diversity influenced EMF and stability over time, and how these effects depended on plant and soil history. Furthermore, during our study period, there was a prolonged period (2018–2019) of extreme drought across Germany (Bastos et al., 2020; Schuldt et al., 2020; van Sundert et al., 2021). We used this naturally occurring weather anomaly to further test the effects of plant community diversity and age on multifunctional resistance and resilience, calculated according to Isbell et al. (2015). We tested the following hypotheses: (1a) EMF increases with plant species richness, and (1b) is higher in old plant communities than in new or re-sown communities. (2a) Plant diversity enhances the temporal stability of EMF, as well as multifunctional resistance and resilience against drought. (2b) This stabilizing effect of diversity is more pronounced in old plant communities than in new or re-sown communities.

2 | MATERIALS AND METHODS

2.1 | Study site—Jena experiment and Δ BEF experiment

The present study was conducted in the Jena Experiment, which is a long-term grassland biodiversity experiment located in the floodplain of the Saale river near the city of Jena in Thuringia,

Germany (50°55' N, 11° 35' E, 130 m a.s.l.; Roscher et al., 2004). Before the experiment was established in 2002, the study area had been used as a high-fertilized arable field for growing wheat and vegetables (1960s–2000; not cultivated in 2001). The soil is a Eutric Fluvisol, while soil texture changes from sandy loam to silty clay with increasing distance to the river. To account for these spatial differences in soil texture, the site was divided into four blocks, arranged in parallel to the riverside (Roscher et al., 2004). For the years 2003–2016, the mean annual air temperature was 9.7°C and the mean annual precipitation was 574 mm, recorded with a meteorological station at the study site (Weather Station Jena-Saaleaue, Max Planck Institute for Biogeochemistry Jena, <https://www.bgc-jena.mpg.de/wetter/>).

For the experiment, 60 native grassland species typical for Central European mesophilic grassland of the Arrhenatherion type (Ellenberg, 1988) were selected and assigned to four functional groups: small herbs (12 species), tall herbs (20 species, respectively), grasses (16 species), and legumes (12 species; Roscher et al., 2004). The Jena Experiment consists of 82 experimental communities differing in plant species richness (1, 2, 4, 8, 16, and 60) and plant functional group number (1, 2, 3, and 4). There are 16 replicates for each species richness level, except for the 60-species mixtures (4 replicates) and the 16-species mixtures (14 replicates). In the latter, this is caused by the fact that it was not possible to create communities consisting only of small herbs or legumes, because there were only 12 species per functional group present in the species pool, respectively. The selection of the species combinations per community was done by random draws from the respective functional group pools. The plant communities were initially growing in 20 × 20 m plots, while the size of the plots was reduced to 6 × 6 m in 2010. Communities were established in 2002 by sowing a total of 1000 viable seeds per m², distributed equally among species in the mixtures. Some species were re-sown in autumn 2002 because of poor germination rates (Roscher et al., 2004). Further sowings did not happen. In 2010, two monocultures were abandoned because of poor establishment (*Bellis perennis* L. and *Cynosurus cristatus* L.; Weisser et al., 2017), which resulted in 14 monoculture plots and a total of 80 plant communities from 2010 onwards. Plots were mown twice a year, in early June and early September, and mown plant material was removed, as it is typical for extensive hay meadow management. To preserve the experimental species richness levels and combinations, plots were weeded two or three times a year (April, July, and October). Weeding did not influence plant diversity effects on ecosystem functions (Weisser et al., 2017). Plots were never fertilized. More detailed information about the design and setup of the Jena Experiment can be found in Roscher et al. (2004) and Weisser et al. (2017).

To test not only plant species richness effects on EMF but also the potential role of community age (i.e., plant and soil history), we conducted our study in the ΔBEF experiment, which is a split-plot experiment within the main plots of the Jena Experiment (Vogel et al., 2019). In each of the 80 main plots, three 3 × 1.5 m subplots were established, which differ in plant and soil history:

- “old plant communities”: soil conditioned since 2002 (i.e., with soil history) and plant communities sown in 2002 (i.e., with plant history); represent the long-term plots of the Jena Experiment);
- “new plant communities”: new soil originated from an arable field (i.e., without soil history) and plant communities sown in 2016 (i.e., without plant history);
- “re-sown plant communities”: soil conditioned since 2002 (i.e., with soil history) and plant communities sown in 2016 (i.e., without plant history).

For the establishment of the “new plant communities”, the original soil was excavated to a depth of 30 cm and replaced by soil from an arable field (same soil layer), which is in the direct vicinity of the field site of the Jena Experiment (Vogel et al., 2019). Similar to the initial conditions of the study site in 2002, the new field soil was rich in nutrients, as the neighboring field is used for growing wheat and vegetables and thus highly fertilized (Vogel et al., 2019). For the establishment of the “re-sown plant communities”, the plant sod was removed by a digger, and soil was mixed and homogenized to a depth of 30 cm to remove bigger roots by hand. To prevent mixing of “old” and “new” arable soil and to prevent that surrounding roots of “old” plants could grow into the new plots, plastic sheets (1 mm thick) were installed as soil barriers (0–30 cm). The soil of newly established plots was recompact using a vibrating plate before the seeding of plant communities. Seeds were sown in new and re-sown plots in May 2016, as done in 2002. Seed material was purchased from the same commercial supplier, which also supplied the seed material in 2002. There was no sowing on old plots in 2016.

2.2 | Long-term precipitation data and drought

During our study period (2017–2021), Central Europe experienced a 2-year drought, which was documented by numerous studies (e.g., Kleine et al., 2021; Rakovec et al., 2022; Schuldt et al., 2020; Smith et al., 2020). Here, we define drought in the meteorological sense (“meteorological drought”) as the deviation of precipitation from a normal value over a certain period of time (Hisdal et al., 2000). Using the mean values of the 14 years prior to the study period as a reference period, we identified drought events in 2018 and 2019 in the Jena Experiment, with a 33% and 13% reduction in precipitation, respectively, and larger than expected precipitation in 2017 (5%), 2020 (2%), and 2021 (9%; precipitation was recorded with the meteorological station located at the Jena Experiment site). As the drought occurred mainly during the hot summer months in 2018 and 2019, we also checked precipitation during the growing season (i.e., the time period when mean daily temperature was larger than 10°C, which differs among years; mainly from April to October, sometimes from May to September or November). Using the growing periods from 2003 to 2016 as a reference period, again, 2018 and 2019 showed a strong reduction in rainfall (44% and 21%, respectively), while precipitation in 2020 was only slightly reduced by 3% and increased in 2017

and 2021 (0.3% and 7%, respectively). Based on this, we categorized the years 2018 and 2019 as “drought years” (first-drought and second-drought years), and the years 2017, 2020, and 2021 as “normal years” (2020: first year after drought, 2021: second year after drought).

2.3 | Data collection

All functions used in this study (to calculate multifunctionality indices) were measured on all 240 subplots on an annual basis (2017–2021), always following the same protocol. Producer-related functions include aboveground biomass and cover of target plant communities as well as invasive plants (i.e., non-target weed species), vegetation height and flower height, and LAI. Aboveground biomass was harvested twice a year at the time of peak biomass (late May and August). Therefore, vegetation was clipped 3 cm aboveground in two randomly placed 0.2 × 0.5 m frames per subplot, then sorted into sown plant species, non-target weeds, and dead plant material, dried at 70°C for 48 h, and weighed. The dried biomass of target species per subsample (i.e., per frame) was summed up to obtain community biomass production values. The biomass values of the target plant community and weeds, respectively, of both subsamples per subplot (i.e., both frames) were averaged per season. Finally, the biomass of May and August harvests was summed to obtain the annual biomass production of sown plant communities and weeds, respectively, and then extrapolated to one square meter ($\text{g m}^{-2} \text{ years}^{-1}$). All other plant-related functions were measured shortly before each biomass harvest. For measuring the LAI, a LAI-2200C Plant Canopy Analyzer (LI-COR, Lincoln, USA) was used. One reference measurement was done above the canopy, and five measurements were taken in the vegetation (approx. 5 cm aboveground) along the diameter of the subplot. The five measurements below the canopy were averaged to obtain one value per season and subplot. The cover of sown plant species and weeds within subplots was estimated by using the decimal scale (based on Londo, 1976). Maximum vegetation height (highest leaves) and maximum flower height (highest flower) were measured five times along a transect, with a ruler, in each subplot. These five measured height values (for vegetation and flower height, respectively) were then averaged to get one value per season. For LAI, plant cover, vegetation height, and flower height May and August values were averaged to get one value per year.

The remaining functions were related to higher-trophic levels and abiotic properties: belowground, we used the functions microbial biomass carbon (C_{mic}), microbial basal respiration (BAS), and soil water availability, and aboveground, herbivory and predation. We considered soil water content as an ecosystem function given that soil water retention is a critical ecosystem property determining biological activity across trophic levels. For belowground functions, four soil cores (diameter: 2 cm; depth: 10 cm) were taken every year in June, pooled per subplot, and stored in plastic bags at 4°C. In the laboratory, soil was sieved (mesh size: 2 mm) and roots or larger animals were sorted out. Finally, microbial biomass carbon,

basal respiration, and soil water availability were measured after Scheu (1992) using an O_2 -microcompensation apparatus (as done in Eisenhauer et al., 2010). For the determination of aboveground herbivory, 20 leaves per plant species were randomly picked from the biomass harvested in August. First, the absolute area damaged by invertebrate herbivores (in mm^2) was estimated by eye using a template card with a range of circles and squares of known size for reference. Second, the leaf area of all 20 leaves per species sample was measured with a leaf area meter (LI-3000C Area Meter, LI-COR Biosciences, Lincoln, Nebraska, USA). Finally, herbivory (%) per year and subplot were calculated following the approach by Loranger et al. (2014) and Meyer et al. (2017). For aboveground predation, five plasticine dummies (in new and re-sown plant communities) and 10 dummies (in old plant communities; larger plots required more sampling points to better cover the spatial heterogeneity in predation pressure) were placed for 24 h in the plots, every August at peak biomass (for more information about the method, see Hertzog et al., 2017; Meyer et al., 2015). Dummies were pinned to needles on the ground with a distance of 20 cm between replicates. After exposure, dummies were checked for predation marks by arthropods; dummies with marks were counted as “1” and non-attacked dummies as “0”. Finally, the percentage of attacked dummies was calculated as the rate of predation per subplot and year.

2.4 | Calculation of EMF indices

First, we imputed missing subplot data for specific functions with the mean value of all other subplots in the particular year. This was necessary for a low number of measurements of microbial activity (C_{mic} = 2.8% missing data, BAS = 0.7%), soil water availability (0.7%), and herbivory (9.2%). To fairly combine all the functions measured in different units and at different scales, we then performed a minimum–maximum (Min–Max) normalization, which resulted in all functions being on a scale between 0 and 1 (Eisenhauer et al., 2018; Wang et al., 2019). Therefore, we used the following equation:

$$x_{\text{transf.}} = \frac{x - x_{\text{min}}}{x_{\text{max}} - x_{\text{min}}}$$

where x is the value of a function for a specific subplot and year being transformed, x_{min} is the lowest, and x_{max} is the highest value of the respective function in the same year. Correlation tests have shown that the data structure has not changed after normalization (i.e., strong positive correlation between data before and after normalization). The Min–Max normalization requires that the functions are normally distributed. To achieve this, we Box–Cox-transformed all functions before we Min–Max-normalized the data. Functions for which lower values indicate higher functioning (i.e., weed cover and weed biomass production) were inverted, that is, the Box–Cox-transformed and Min–Max-normalized values per subplot and year were subtracted from 1 (Maestre et al., 2012). After data transformation and normalization, we tested whether the different functions correlated with each other and found a significant positive

correlation for 14 out of 132 possible combinations with correlation coefficients (r) ranging from .5 to .9. To reduce the influence of highly correlated functions on EMF, we averaged these functions per subplot and year: target plant cover and plant biomass were averaged, resulting in a new function named plant community performance; weed cover and weed biomass (both inversed) were averaged, resulting in the function plant invasion resistance; and vegetation and flower height were averaged, resulting in the function plant community height. In this way, we reduced the number of significant correlations to two (plant community performance and invasion resistance [$r = .71$], as well as plant community performance and plant community height [$r = .68$]).

These calculations resulted in four plant-related functions (plant community performance, invasion resistance, plant community height, LAI), four functions related to higher-trophic levels (soil microbial biomass [C_{mic}], soil microbial respiration [BAS], aboveground herbivory, aboveground predation), and one abiotic function (soil water availability), each ranging between 0 and 1 (Table S1). Finally, to calculate EMF, we used two approaches: the averaging and the multiple threshold approach, as both are widely used in EMF research (Byrnes et al., 2014; Maestre et al., 2012; Manning et al., 2018; Meyer et al., 2018). For the averaging approach, all nine functions were averaged per subplot and year, resulting in an EMF index ranging between 0 and 1. For the multiple threshold approach, we first determined the total number of functions (max. 9) that exceeded a critical threshold, while the threshold was defined as a certain percentage of the highest performance of each function (i.e., maximum level of functioning). Thereby, we followed the recommendation by Byrnes et al. (2014) that the maximum level of functioning was calculated as the average of the five plots with the highest values to minimize bias by potential outliers. In our study, we used nine different thresholds (10%, 20%, 30%, ..., 90%) to represent a wide spectrum in our analysis (Soliveres et al., 2016). Finally, with the multiple threshold approach, we got EMF indices ranging between 0 and 9 for each threshold, subplot, and year. As both approaches showed similar patterns (Table S2, Figure S1), further analyses were done using the EMF index calculated by averaging, as it is more suitable for linear model analysis (Byrnes et al., 2014).

To test whether plant-related EMF responded differently than EMF at higher-trophic levels and to exclude the possibility that total EMF is biased by stronger consideration of plant-related functions (due to higher interrelationships), we calculated two separate EMF indices in addition to total EMF: plant-related EMF and higher-trophic level EMF (i.e., sensitivity analysis; Tables S3–S5, Figures S2–S5). To calculate these two, we used the same averaging method as for total EMF.

2.5 | Calculation of temporal stability, resistance, and resilience of EMF

For the calculation of temporal stability from 2017 to 2021, we divided the standard deviation of EMF by the mean values of EMF

(Pimm, 1984; Tilman, 1999; Tilman et al., 2006). Higher temporal stability can be explained by high mean values and/or by low SD (Craven et al., 2018).

For the calculation of resistance and resilience, we used the method proposed by Isbell et al. (2015):

$$\text{Resistance} = \frac{\bar{Y}_n}{|Y_e - \bar{Y}_n|}$$

$$\text{Resilience} = \frac{|Y_e - \bar{Y}_n|}{|Y_{e+1} - \bar{Y}_n|}$$

where \bar{Y}_n are the values during normal years, Y_e are values during climate event, and Y_{e+1} values after the climate event. As the communities in our study experienced a 2-year drought event, we tested whether multifunctional resistance in the first year differs from resistance in the second-drought year. Therefore, we calculated a “first-year multifunctional resistance” and a “second-year multifunctional resistance”. For both types of multifunctional resistance, we used the 2017 values for \bar{Y}_n (“normal years”), while for Y_e (“climate event year”), we used the 2018 values for first-year multifunctional resistance calculation, and the 2019 values for second-year multifunctional resistance calculation (calculation for each subplot; Figure 1a,b; Table S1). For multifunctional resilience calculations, we used a similar approach, because we wanted to test whether EMF resilience differed in the first and in the second year after drought (i.e., “first-year EMF resilience” vs. “second-year EMF resilience”; Figure 1c,d; Table S1). Again, we used the 2017 values for \bar{Y}_n . For Y_e , we used the 2019 values for both types of multifunctional resilience, as it was the year with the lowest EMF values, that is, peak of the drought event; for Y_{e+1} (“years after climate event”), we used the 2020 values for first-year multifunctional resilience calculation, and the 2021 values for second-year multifunctional resilience calculation (calculation for each subplot; Figure 1c,d; Table S1).

To test whether 2017 was a “normal” year, we analyzed the mean aboveground plant biomass production of the old communities from 2012 to 2021. We found that plant biomass production in 2017 was within the range of biomass production from 2012 to 2016, while it decreased in 2018 and 2019 to values below the range from 2012 to 2016 (Figure S19). As plant biomass production is one of the most important and frequently used indicators of ecosystem functioning and is directly or indirectly related to many other functions, we thus consider 2017 to be a “normal” year.

2.6 | Statistical analysis

To test whether plant species richness, history treatment, and year had an impact on total EMF, as well as temporal stability of EMF, multifunctional resistance, and multifunctional resilience, we fitted linear mixed-effects models. We used block, plot, the interaction of plot and history treatment (= subplot), and the interaction of plot and year (as factor) as random effects and started

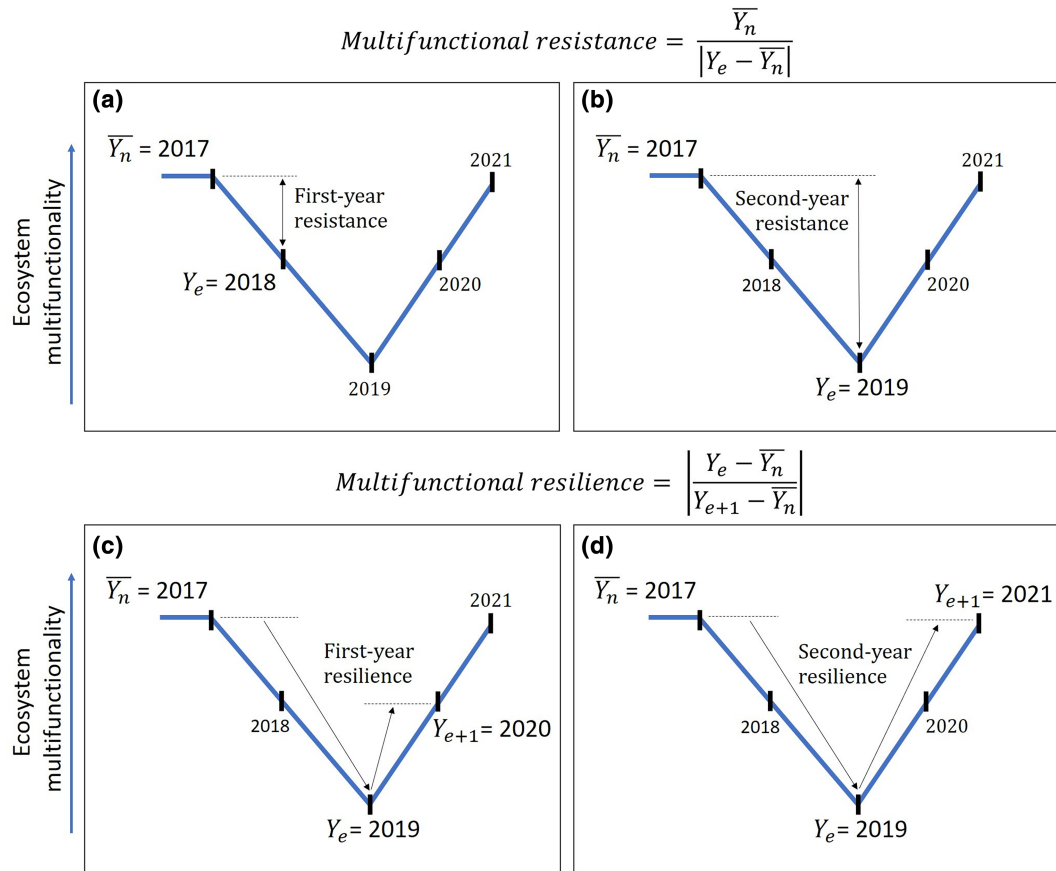


FIGURE 1 Schematic illustration showing how we calculated multifunctional resistance and resilience according to Isbell et al. (2015). For this method, the following components were used: \bar{Y}_n as the values during normal years, Y_e as values during climate event, and Y_{e+1} as values after the climate event. Because our study period included two drought years (2018, 2019) and two post-drought years (2020, 2021), we calculated resistance and resilience in the first and second year of drought/post-drought, respectively. For first-year multifunctional resistance (a), we used the 2017 values for \bar{Y}_n (“normal years”), and the 2018 values for Y_e (“climate event year”). For second-year multifunctional resistance (b), we again used the 2017 values for \bar{Y}_n , and the 2019 values for Y_e . For first-year multifunctional resilience (c), we also used the 2017 values for \bar{Y}_n , the 2019 values for Y_e (year with the lowest EMF) and the 2020 values for Y_{e+1} (“years after climate event”). For second-year multifunctional resilience (d), we used the 2017 values for \bar{Y}_n , the 2019 values for Y_e , and the 2021 values for Y_{e+1} .

with a null model with these random effects only. Then, we added the fixed effects in a stepwise order: year (2017–2021 [as factors] for EMF; first vs. second year for EMF resistance and resilience), followed by plant species richness (SR; 1, 2, 4, 8, 16, 60; log-transformed), history treatment (HT; old, new, re-sown), and all possible interactions (year \times SR, year \times HT, SR \times HT, year \times SR \times HT; Text S1). Because we found several significant year \times plant species richness and year \times history treatment effects on multifunctional resistance and resilience (Table 1), we further analyzed first-year and second-year variables in separate models (without year as fixed effect). Therefore, we used block and plot as random effects, and species richness (log-transformed), history treatment, and their interaction as fixed effects, which were again added stepwise. Temporal stability of EMF was analyzed in the same way (because stability was calculated over years, this variable obviously could not be used as explanatory).

Prior to these analyses, we log-transformed temporal stability, as well as multifunctional resistance and resilience variables to achieve normality for the residuals. All models were fitted with

maximum likelihood (ML), and likelihood ratio tests were used to decide on the significance of the fixed effects. Moreover, we used Tukey’s HSD tests to check for differences among history treatments. All calculations and statistical analyses were done in R (version 3.6.1, R Development Core Team, <http://www.R-project.org>), including the package lme4 (Bates et al., 2015) for mixed-effects model analysis, and multcomp (Hothorn et al., 2016) for Tukey HSD tests.

3 | RESULTS

3.1 | Effects of plant species richness, history treatment, and year on EMF

We found a significant impact of all three variables on EMF (Table 1). Over years, EMF showed a v-shaped development, that is, it decreased from 2017 to 2019, but recovered in 2020 and 2021 to a value that was close to the value in 2017 (Figure 2). Plant species

TABLE 1 Summary of mixed-effects model analyses testing the effects of year, plant species richness (SR), history treatment (HT), and their interactions on ecosystem multifunctionality (a), temporal stability of ecosystem multifunctionality (b), multifunctional resistance (c), and multifunctional resilience (d). Models were fitted by adding fixed effects stepwise (the first model is the null model, the second model contains the first fixed effect (i.e., first listed fixed effect in the table), the third model contains the first and the second fixed effect (second listed fixed effect in the table), and so on). Shown are the results of the likelihood ratio tests (degrees of freedom [df], χ^2), which were applied to assess the model improvement and the statistical significance of the fixed effects (*p*-values). Significant effects (*p* < .05) are given in bold and marginally significant effects (*p* < .1) are in italics. Note that for the fixed effect year, we used the study years 2017–2021 (as factor) for ecosystem multifunctionality, the drought years 2018 and 2019 (first- vs. second-drought year) for multifunctionality resistance, and the post-drought years 2020 and 2021 (first vs. second post-drought year) for multifunctionality resilience. For temporal stability of ecosystem multifunctionality, year was not contained in the dependent variable and thus not used as explanatory.

	df	χ^2	<i>p</i>
(a) Ecosystem multifunctionality			
Year (2017–2021)	4	328.92	<.001
Species richness (SR)	1	77.94	<.001
History treatment (HT)	2	93.72	<.001
Year × SR	4	18.84	.001
Year × HT	8	29.71	<.001
SR × HT	2	24.54	<.001
Year × SR × HT	8	14.23	<i>.076</i>
(b) Temporal stability of ecosystem multifunctionality			
Species richness (SR)	1	26.30	<.001
History treatment (HT)	2	6.82	.033
SR × HT	2	3.97	<i>.138</i>
(c) Multifunctional resistance			
Year (first vs. second)	1	40.23	<.001
Species richness (SR)	1	17.24	<.001
History treatment (HT)	2	0.07	<i>.967</i>
Year × SR	1	4.20	.040
Year × HT	2	0.26	<i>.880</i>
SR × HT	2	1.38	<i>.502</i>
Year × SR × HT	2	1.12	<i>.572</i>
(d) Multifunctional resilience			
Year (first vs. second)	1	18.19	<.001
Species richness (SR)	1	0.31	<i>.580</i>
History treatment (HT)	2	2.46	<i>.293</i>
Year × SR	1	2.21	<i>.138</i>
Year × HT	2	3.96	<i>.138</i>
SR × HT	2	0.40	<i>.817</i>
Year × SR × HT	2	2.88	<i>.237</i>

richness significantly increased EMF, whereby the slope of the regression line varied slightly from year to year (Table 1, Figure 3).

Furthermore, EMF differed significantly among the three history treatments: old and new plant communities showed higher EMF than re-sown communities (Table 1; Figures 2b and 3b). This was consistent over the entire study period except in 2020, where old communities showed the highest, new communities an intermediate, and re-sown communities the lowest EMF (significant year × history treatment interaction; Table 1, Figure 2b). Old, new, and re-sown plant communities also differed in their biodiversity–EMF relationship: the positive effect of plant species richness on EMF was significantly stronger in old plant communities compared with new or re-sown communities (significant plant species richness × history treatment interaction; Table 1, Figure 3b). Furthermore, the relationship between plant species richness and EMF strengthened from 2017 to 2021 in new and re-sown plant communities, respectively, while in old communities the relationship was already strong in 2017, slightly decreased from 2017 to 2020, and finally recovered to a value higher than that in 2017 (marginal significant three-way interaction; Table 1; Figure 3b).

Similar to total EMF, we additionally calculated plant-related and higher-trophic level EMF (using only plant-related and higher-trophic level functions, respectively) to check whether they differ in their response (i.e., sensitivity analysis; Table S1). Over time, both EMF types changed, that is, both decreased from 2017 to 2019, but while higher-trophic level EMF recovered in 2020 and 2021 to higher values than the initial values in 2017, plant-related EMF remained at low levels (Table S6, Figure S6a,b). We found positive effects of plant species richness on both EMF types, while in general, plant-related EMF showed a stronger relationship with plant species richness than higher-trophic level EMF (Table S6, Figure S7a,b). Regarding history treatments, we found that plant-related EMF was significantly higher in new plant communities than in old and re-sown communities, while higher-trophic level EMF was highest in old communities, intermediate in new communities, and lowest in re-sown communities (Table S6, Figure 2c,d). The relationship between both EMF types and plant species richness was positive in all three history treatments, while the strength was the highest in old plant communities (Table S6, Figure S7c,d). Results of analyses with single functions can be found in Figures S8–S16.

3.2 | Effects of plant species richness and history treatment on temporal stability of EMF, as well as multifunctional resistance and resilience

Temporal stability increased with plant species richness (Table 1, Figure 4a), related to an increase in the mean of total EMF with plant species richness, while the standard deviation (SD) of EMF did not change (Table S7, Figure S17). Regarding history treatments, we found that old plant communities showed the highest temporal stability of EMF, while new and re-sown communities had similarly lower values (Table 1, Figure 4b). High mean values and low SD can explain high temporal stability in old plant communities. Lower temporal stability in new plant communities was

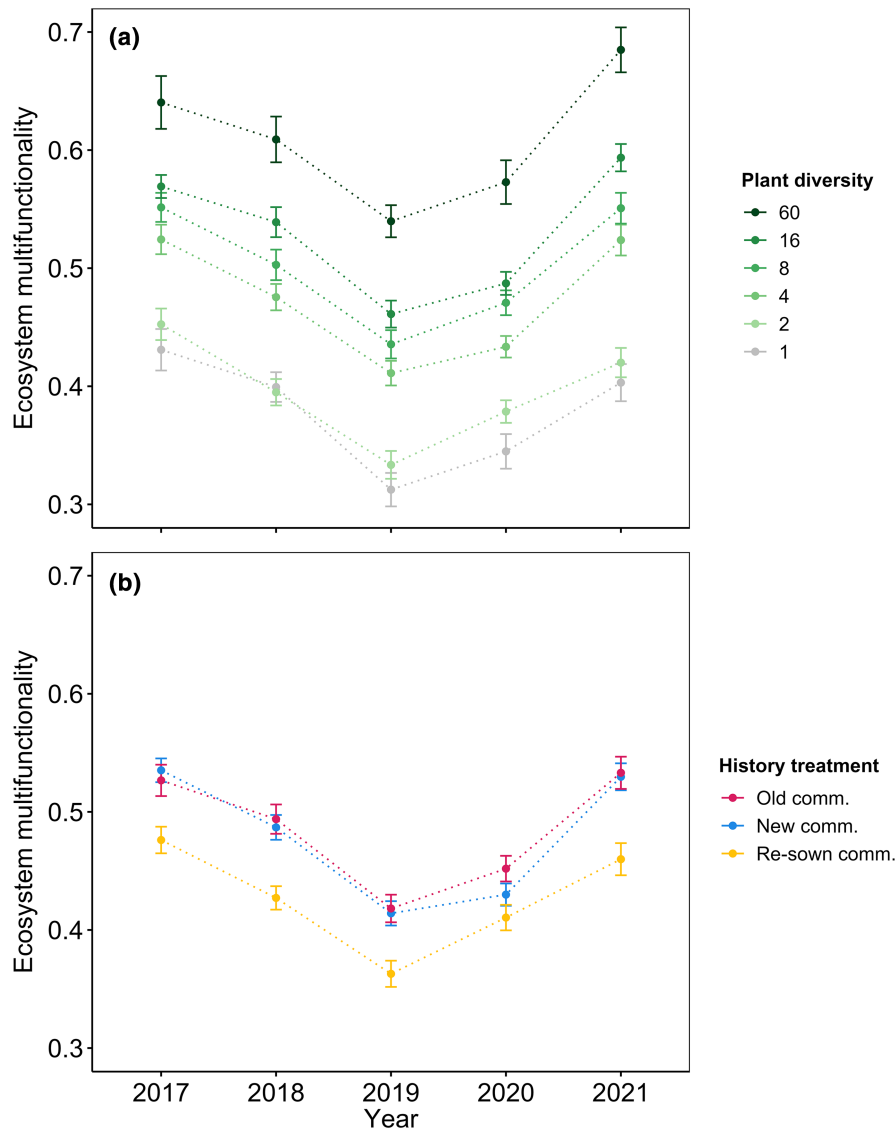


FIGURE 2 Changes in ecosystem multifunctionality over the study period (2017–2021) for the different plant species richness levels (1–60; a) and for the history treatments (old, new, and re-sown communities; b). Shown are means \pm 1 SE, and colors in (b) indicate the different history treatments. Note that the dotted lines were drawn for visualization. In the mixed-effects models, year was used as factor.

mainly caused by high SD (while mean values were also high), and in re-sown communities by low mean values and high SD (Tables S1 and S7; Figure S18).

Multifunctional resistance was higher in the first year (2018) than in the second year (2019; Table 1; Figure 5a). Moreover, multifunctional resistance increased with plant species richness in both drought years but did not differ among history treatments (Table 1; Figure 5a; Table S8). Multifunctional resilience was higher in the second year after the drought (2021) than in the first year (2020) but did not differ along the plant species richness gradient or among history treatments (Table 1; Figure 5b; Table S8).

In terms of plant-related and higher-trophic level EMF, we found that plant species richness increased temporal stability, resistance, and resilience of both types of EMF, except resilience of higher-trophic level EMF, which decreased with plant species richness (Tables S3–S5). Moreover, old plant communities showed higher temporal stability of both types of EMF and a higher resistance of plant-related EMF, while new and re-sown plots had lower values (Tables S3–S5). A more detailed description for

multifunctional stability, resistance, and resilience using plant-related and higher-trophic level EMF can be found in Text S2, Tables S3–S5, Figures S2–S5.

4 | DISCUSSION

4.1 | Biodiverse and old plant communities provide higher EMF

Our findings clearly show that EMF increased with plant species richness, which is in line with previous studies (Eisenhauer et al., 2018; Hector & Bagchi, 2007; Meyer et al., 2018). Furthermore, our findings suggest that this positive relationship is affected by soil and plant history, which had been shown for single ecosystem functions (Guerrero-Ramírez et al., 2017; Huang et al., 2023; Reich et al., 2012), but never for EMF.

In recent years, several processes have been identified that contribute to the positive relationship between plant diversity and biomass

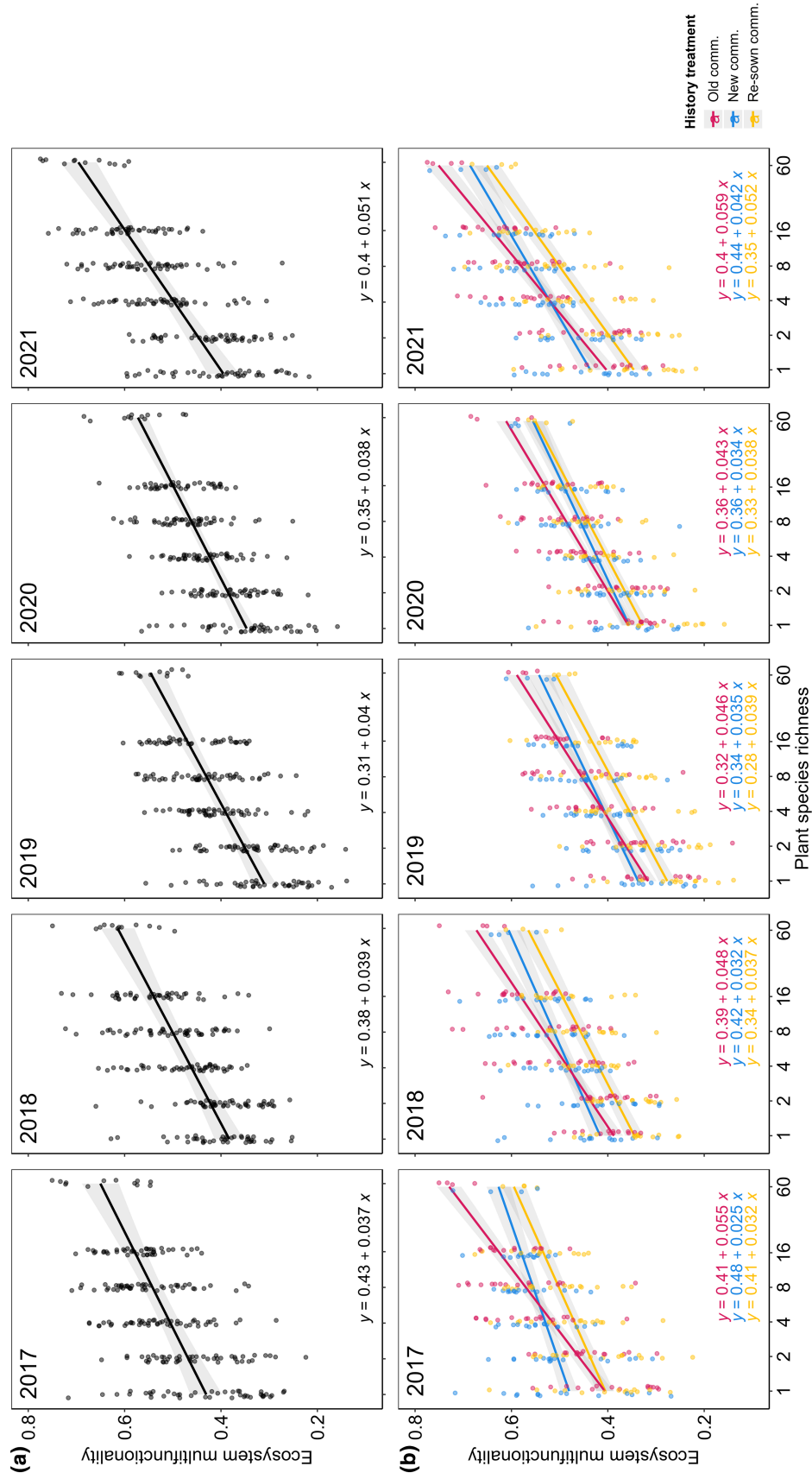


FIGURE 3 Ecosystem multifunctionality as a function of log-transformed plant species richness over all plant communities (a) and separately for the different history treatments (old, new, and re-sown communities; b) in the years 2017–2021. Each dot represents a plant community, and colors indicate the different history treatments. Regression lines are based on mixed-effect models (predicted means). Solid lines indicate significant relationships ($p < .05$), and gray shades are standard errors. In the bottom-right corner are the regression line equations.

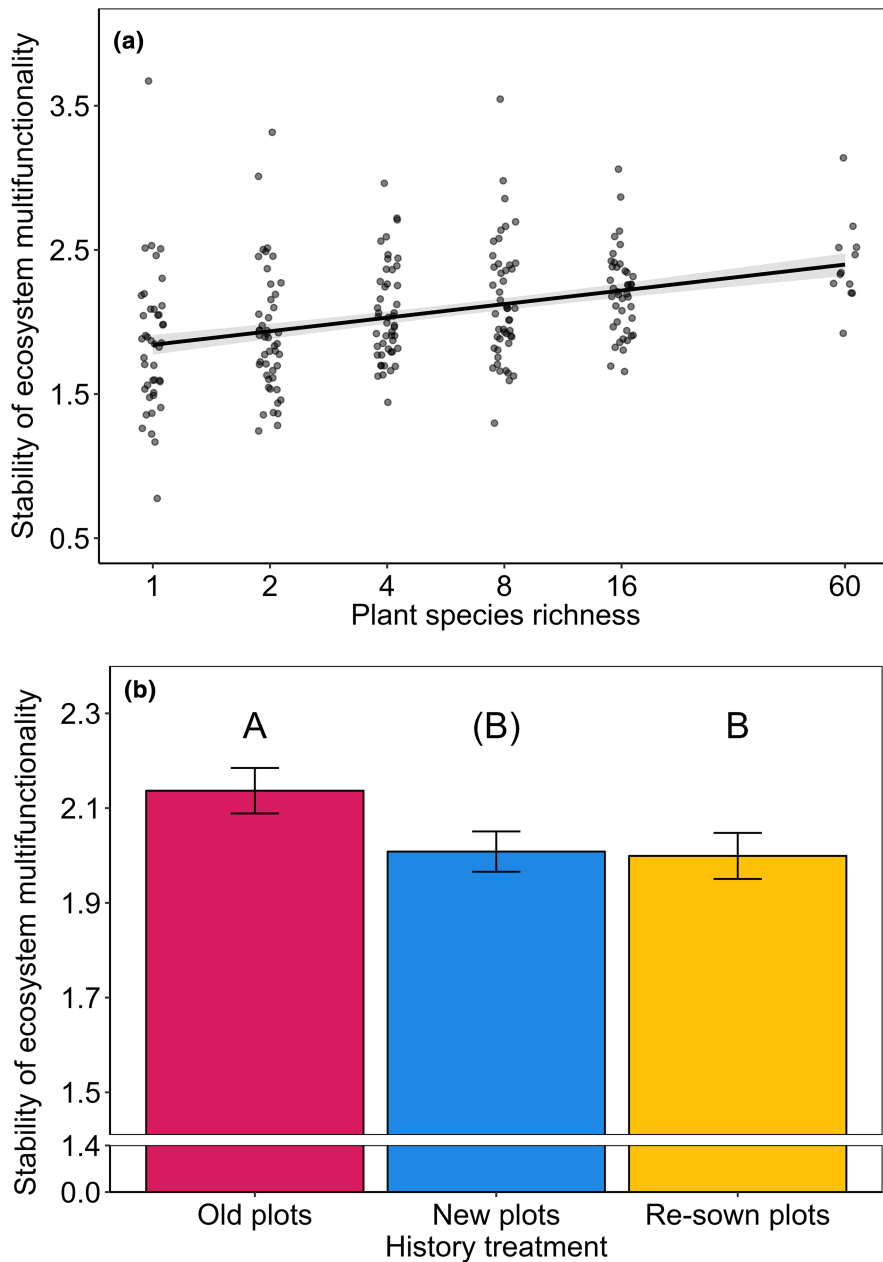
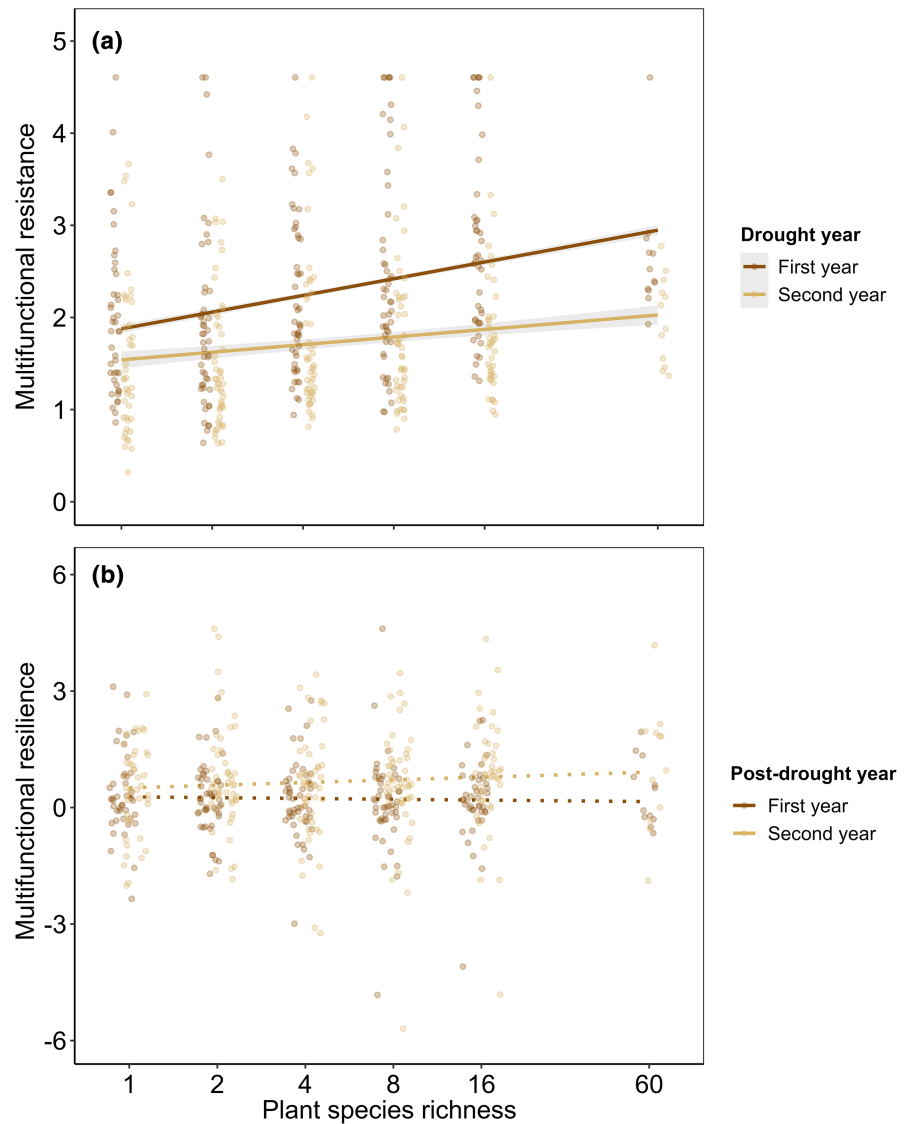


FIGURE 4 Temporal stability of ecosystem multifunctionality (log-transformed) as a function of log-transformed plant species richness (a) and as bar plot for the different history treatments (old, new, and re-sown communities; b). Each dot in (a) represents a plant community; regression line is based on mixed-effects model (predicted means). Solid line indicates significant relationship ($p < .05$), and gray shade is SE. Bars in (b) show mean values (± 1 SE); letters without brackets above bars indicate significant ($p < .05$) differences among history treatments, letters with brackets indicate marginally significant ($.05 < p < .1$) differences (Tukey's HSD test).

production, which may also have validity for the development of the biodiversity–EMF relationship with increasing community age. Among others, microevolutionary processes have recently been recognized to play a significant role in this development (Eisenhauer et al., 2019), that is, plant and soil communities adjust to each other over time, increasing plant community productivity (Dietrich et al., 2021; Hahl et al., 2020; van Moorsel et al., 2021; Zuppinger-Dingley et al., 2014). This is confirmed by the results of our history treatments. In old plant communities, with a joint plant and soil history, we found a higher EMF (and a stronger biodiversity–ecosystem multifunctionality [BEM] relationship) than in re-sown plant communities, where plants and soil organisms were not adjusted to each other. Consequently, a lower degree of adaptation leads to smaller positive soil–biota effects on plant growth (also known as positive plant–soil feedbacks) in re-sown than in old communities.

In contrast to re-sown plant communities, new communities showed a similar high EMF as old communities (but also a weaker BEM relationship; Figure 2b). Sensitivity analysis revealed that different underlying patterns cause the high multifunctionality values in old and new communities, respectively: new plant communities are characterized by the highest values of plant-related functions but low values of higher-trophic level functions. Old plant communities, in contrast, show the opposite (Figure S6). These different patterns can be explained by two aspects: (i) nutrient availability, that is, nutrient-rich agricultural soil, was used for the establishment of new plant communities (Vogel et al., 2019), which allowed plants to grow at high rates (i.e., high values of plant-related functions in the beginning). High nutrient levels could also explain why the BEM relationship was weaker in these communities, confirming previous studies (Harpole et al., 2016; Humbert et al., 2016; Verma &

FIGURE 5 Multifunctional resistance (a) and resilience (b; both log-transformed) as a function of log-transformed plant species richness. Each dot represents a plant community; and colors indicate multifunctional resistance and resilience during the first and second year of drought/post-drought. Regression lines are based on mixed-effects models (predicted means). Solid lines indicate significant relationships ($p < .05$), gray shades are standard errors, and dotted lines indicate non-significant relationships ($p > .1$).



Sagar, 2020). Furthermore, the different patterns can be explained by (ii) a time lag effect of higher-trophic organisms causing that related functions also need time to occur (i.e., higher values of higher-trophic level functions at later stages; Eisenhauer et al., 2010).

4.2 | Temporal stability, resistance, and resilience of EMF increase in biodiverse and old plant communities

We found a positive effect of plant species richness on the temporal stability of EMF, which is in line with Jing et al. (2022) (but see also Sasaki et al., 2019). This positive relationship is mainly explained by an increase in the mean of EMF, while its SD did not differ along the plant species richness gradient. This shows that high performance of species-rich communities (i.e., higher values of functions compared to species-poor communities), and thus a higher buffering potential, is responsible for high temporal stability—a result that was

rarely found for single functions (e.g., biomass production; Hautier & van der Plas, 2022). In addition, sensitivity analysis revealed that fluctuation plays a role: next to an increase in mean, the SD of plant-related EMF significantly decreased with plant species richness (Figure S2), which indicates that these functions fluctuate less over the years, implying that higher stability in species-rich communities was caused by a general overperformance of functions as well as a lower fluctuation of plant-related functions over the years.

Furthermore, we found significant differences in temporal stability in old, new, and re-sown plant communities. Old communities showed a higher temporal stability of EMF than new and re-sown communities, which was explained by a high mean and low SD of EMF. New communities are also characterized by a high mean of EMF, but the SD was high as well, demonstrating that new communities were more unstable due to greater fluctuations over the years. This suggests that the increase in multifunctional stability over time is caused by a decrease in fluctuations, probably induced by adjustment processes between plant species and higher-trophic organisms

over time. Similar conclusions were also drawn in a recent study by Wagg et al. (2022), which investigated the stability of biomass production over the last 20 years in the Jena Experiment. In contrast to new communities, re-sown communities had low stability due to a low mean EMF, while the standard deviation was also low (i.e., low fluctuation over the years). This indicates that low stability in re-sown communities was mainly caused by generally low values of functions found in these communities, caused by low nutrient content in the soil ("old soil") as well as a lack of adaptation between soil and the plant community ("new seeds").

Multifunctional resistance decreased with the duration of the 2-year drought, while after drought, EMF recovered stepwise to pre-drought levels, that is, multifunctional resilience increased with year. These results are an important insight, as an increasing number of studies show that extreme weather events will last longer and be more frequent under ongoing global change (Mahecha et al., 2022; Pörtner et al., 2022). In relation to our results, this implies that prolonged droughts can lead to a considerable decline in the level and resistance of EMF, which may not recover to pre-event levels due to more frequent events (i.e., low resilience due to shorter recovery periods).

Moreover, we found positive effects of plant species richness on multifunctional resistance. We are not aware of any other study that has tested this before, but there is one study that has shown that functional diversity of leaf traits has a positive effect on multifunctional resistance (Valencia et al., 2015), supporting our findings. Our results underpin the hypothesis that various species are needed to maintain high multifunctionality in a changing world (Eisenhauer et al., 2018), as certain species can maintain or induce functions that other species cannot provide under extreme conditions (Isbell et al., 2011). Furthermore, we found that plant-related resistance was greater in old plant communities than in new or re-sown communities. Similar results were also found in a previous study (van Moorsel et al., 2021), which showed that old communities had greater biomass recovery after disturbance (flooding) than new communities. It was also shown that old communities were generally more stable over time (in terms of biomass production), which is another consistent finding with our study. These two independent studies show that community age, and thus microevolutionary processes, have a major influence on how plant communities respond to disturbance.

Resilience of plant-related EMF is positively related to plant diversity, while resilience of higher-trophic level EMF shows a negative relationship (Figure S4). This negative relationship can be explained as follows: After drought, higher-trophic level functions (especially microbial activity) increased in all communities (i.e., were higher than before drought), whereby the increase was greater in species-rich than in species-poor communities. Higher microbial activity after drought can be explained by the fact that rewetting releases microorganisms from stress, and typically creates a resource pulse (Schimel, 2018), while a generally more diverse microbial community in plant mixtures (Schmid et al., 2021) can explain the stronger increase in species-rich plant communities. As a result, and due to the way resilience was

calculated, higher-trophic level EMF resilience decreases with increasing diversity, even though there was a positive diversity effect (Isbell et al., 2015). We conclude from the results that plant diversity increased plant-related and higher-trophic EMF resilience. It is conceivable that higher microbial activity after drought in species-rich plant communities results in faster and better plant regeneration, as more nutrients are released, which is a possible explanation for the "over-compensatory" recovery after drought previously found in the Jena Experiment (Wagg et al., 2017). Overall, our results show for the first time that plant diversity and community age positively influence the stability, resistance, and resilience of EMF, whereas the underlying processes are not yet fully explored. Further studies need to be conducted in biodiversity experiments, whereby regular recording of all scales of the experiment is urgently needed to better understand these relationships (Trogisch et al., 2017).

5 | CONCLUSION

Our study demonstrates the high importance of plant species richness for EMF and its temporal stability, resistance, and resilience. Moreover, we were able to show for the first time that increasing community age has a stabilizing effect on EMF, confirming results from an earlier independent experiment at the same site regarding plant community biomass stability after a flooding event (van Moorsel et al., 2021). The fact that high plant diversity and shared plant and soil history make plant communities less vulnerable to extreme events indicates their importance in the face of current dramatic biodiversity loss and ongoing global climate change. Thus, our study highlights the need of protecting old, species-rich grasslands to maintain high EMF under climate change.

AUTHOR CONTRIBUTIONS

Peter Dietrich: Conceptualization; data curation; formal analysis; investigation; visualization; writing – original draft. **Anne Ebeling:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing. **Sebastian T. Meyer:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; supervision; writing – review and editing. **Ana Elizabeth Bonato Asato:** Data curation; investigation; writing – review and editing. **Maximilian Bröcher:** Data curation; investigation; writing – review and editing. **Gerd Gleixner:** Data curation; funding acquisition; investigation; writing – review and editing. **Yuanyuan Huang:** Data curation; formal analysis; funding acquisition; project administration; writing – review and editing. **Christiane Roscher:** Data curation; funding acquisition; investigation; writing – review and editing. **Bernhard Schmid:** Formal analysis; funding acquisition; writing – review and editing. **Anja Vogel:** Data curation; funding acquisition; project administration; writing – review and editing. **Nico Eisenhauer:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT


The data used in this study are publicly available in the Jena Experiment data portal (<https://jexis.idiv.de/>): (Dietrich et al., 2024b). Raw data of ecosystem functions used to calculate ecosystem multifunctionality are publicly available at <https://doi.org/10.25829/BJG8-G685> (Dietrich et al., 2024a; Huang et al., 2023).

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SUPPORTING INFORMATION

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