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Tree diversity effects on soil microbial biomass and respiration are context dependent across forest diversity experiments

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Abstract

Aim: Soil microorganisms are essential for the functioning of terrestrial ecosystems. Although soil microbial communities and functions are linked to tree species composition and diversity, there has been no comprehensive study of the generality or context dependence of these relationships. Here, we examine tree diversity–soil

Laboratory work was carried out at the Institute of Ecology, Friedrich-Schiller-University Jena, Dornburger Straße 159, 07749 Jena, Germany.

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microbial biomass and respiration relationships across environmental gradients using a global network of tree diversity experiments.

Location: Boreal, temperate, subtropical and tropical forests.

Time period: 2013.

Major taxa studied: Soil microorganisms.

Methods: Soil samples collected from 11 tree diversity experiments were used to measure microbial respiration, biomass and respiratory quotient using the substrate-induced respiration method. All samples were measured using the same analytical device, method and procedure to reduce measurement bias. We used linear mixed-effects models and principal components analysis (PCA) to examine the effects of tree diversity (taxonomic and phylogenetic), environmental conditions and interactions on soil microbial properties.

Results: Abiotic drivers, mainly soil water content, but also soil carbon and soil pH, significantly increased soil microbial biomass and respiration. High soil water content reduced the importance of other abiotic drivers. Tree diversity had no effect on the soil microbial properties, but interactions with phylogenetic diversity indicated that the effects of diversity were context dependent and stronger in drier soils. Similar results were found for soil carbon and soil pH.

Main conclusions: Our results indicate the importance of abiotic variables, especially soil water content, for maintaining high levels of soil microbial functions and modulating the effects of other environmental drivers. Planting tree species with diverse water-use strategies and structurally complex canopies and high leaf area might be crucial for maintaining high soil microbial biomass and respiration. Given that greater phylogenetic distance alleviated unfavourable soil water conditions, reforestation efforts that account for traits improving soil water content or select more phylogenetically distant species might assist in increasing soil microbial functions.

KEYWORDS

aboveground–belowground interactions, biodiversity–ecosystem functioning, biodiversity loss, context dependence, global change, soil biota, soil microbial functions, soil microorganisms, tree diversity, TreeDivNet

1 | INTRODUCTION

Soil microorganisms are the functional backbones of terrestrial ecosystems (van der Heijden et al., 2008) because they underpin crucial ecosystem functions and services that humans rely upon (Wall et al., 2015). Given the crucial role of soil microorganisms in carbon (C) dynamics and soil feedback effects on climate, improving our current understanding of the drivers of microbial biomass and activity is an essential step towards predicting the impacts of global change (Chen et al., 2019; Serna-Chavez et al., 2013; Xu et al., 2013, 2017). Soil microbial biomass can serve as a proxy for nutrient cycling and soil enzyme dynamics, such as soil organic matter (SOM) turnover, and for secondary productivity. In addition, *in situ* measurements of microbial activity have been shown to be correlated with rates of soil C sequestration (Lange et al., 2015). Together, microbial biomass

and activity provide crucial information on a range of important soil ecosystem functions.

Globally, abiotic factors are thought to be the main drivers of soil microbial biomass and microbial activity (Serna-Chavez et al., 2013; Smith et al., 2021; Wan et al., 2021; Xu et al., 2017). Optimal soil water content (SWC; i.e., soil water-holding capacity of c. 60%), neutral soil pH and high soil organic C content (here summarized as high soil quality) are among the most important factors that directly increase soil microbial biomass and activity (Schimel, 2018). In contrast, climatic conditions, such as temperature, can influence soil microbial biomass indirectly via evapotranspiration and changes in SOM content (Serna-Chavez et al., 2013).

These patterns become less clear when taking interactions among different drivers into account. For instance, the positive effects of high soil nutrient content can be constrained by stressful

TABLE 1 List of tree diversity experiments that contributed to the study (in alphabetical order) to investigate abiotic and biotic drivers of soil microbial functions

Experiment	Country	Biome	Age (years)	Elevation (m)	Former land use	Number of sites	Number of blocks	Number of diversity levels
Bangor	UK	Temperate	9	1	Forest	1	2	3
BEF-China	China	Subtropical	4	190	Forest	2	NA	5
BIOTREE-FD	Germany	Temperate	10	400–415	Pasture	1	4	4*
FORBIO	Belgium	Temperate	3	398, 56, 13	Forest, arable land	3	6	4
IDENT Auclair	Canada	Temperate	3	333	Pasture	1	4	3
IDENT Cloquet	USA	Temperate	3	383	Forest	1	4	3
Kreinitz	Germany	Temperate	8	115	Agricultural	1	2	5
ORPHEE	France	Temperate	5	60	Forest	1	2 [8]	5
SABAH	Borneo	Tropical	11	102	Forest	1	NA [2]	2
Sardinilla	Panama	Tropical	10	70	Forest	2	6	3
SATAKUNTA	Finland	Boreal	14	35	Forest	3	NA	4
Mean ± SD			7.2 ± 3.9	183.6 ± 163.8				3.7 ± 1.0

Note: Abbreviation: NA: Not applicable.

All experiments differ in their plot architecture, as indicated by different numbers of diversity levels and the gradient of diversity. Furthermore, experiments differ in experimental age (in years), number of sites and blocks, plot size, tree distance, tree density and species pool. For the BEF-China and SABAH experiments, only a fraction of the whole diversity gradient was sampled (the respective missing richness levels are indicated by square brackets). The BIOTREE-FD experiment has only one species richness level (with four species per plot), but mixtures differ in their functional diversity (FD; indicated by an asterisk). The number of plots considers only plots that entered the analysis (i.e., controls without trees and plots with missing measurements were excluded). The total number of existing plots is given in square brackets.

environments (Serna-Chavez et al., 2013) or become even stronger (Guerrero-Ramírez et al., 2017), highlighting the importance of context-dependent effects or microclimatic conditions regulated by the vegetation (Gottschall et al., 2019). Moreover, the effects of abiotic drivers can be modulated further by local biotic conditions. For example, studies in grasslands and forests have demonstrated that plant diversity affects soil microbial community composition, activity and biomass (Chen et al., 2019; Lange et al., 2015), with significant effects on ecosystem functions, such as soil carbon storage (Lange et al., 2015).

Nonetheless, global analyses of the effects of plant diversity on soil microbial communities have had limited scope, focusing either on soil communities but not on soil functions, or on grasslands only (Prober et al., 2015; Thakur et al., 2015). In addition, the magnitude and direction of the effects of plant diversity on soil microbial communities were inconsistent, probably owing to the strengthening of these effects with time (Thakur et al., 2015) and different environmental contexts, such as different soil conditions (Guerrero-Ramírez et al., 2017). So far, the effects of plant diversity on soil microbial functions have been studied mostly in grasslands, whereas little is known about the effects of tree diversity on soil microbial functions in forests (Chen et al., 2019; Xu et al., 2020). This is a major knowledge gap, because there might be substantial differences between ecosystems in terms of soil microbial function and potential climate feedback effects on soil communities (Chen et al., 2018).

Previous studies on the effects of tree diversity on soil microorganisms mainly compared monoculture stands with mixtures of two tree species in different environments, making it difficult to

disentangle site conditions from tree diversity and tree identity effects (Liang et al., 2016). One of the first studies using data from a tree diversity experiment with homogeneous abiotic conditions found soil microbial activity and biomass to increase with tree species richness in a saturating relationship, while soil microbial community composition did not vary significantly (Khlifa et al., 2017). One of the potential mechanisms underlying a positive effect of plant diversity on microorganisms is the increased input of diverse resources (Eisenhauer et al., 2017). In line with the view that the quality of plant inputs is essential for soil microbial processes, the chemical composition of leaf litter determines nutrient mineralization, microbial respiration and microbial biomass (Pei et al., 2017), whereas species diversity per se has been shown to have little effect (Meier & Bowman, 2008). This finding suggests that an increase in species richness might not increase soil microbial biomass and activity if not accompanied by a simultaneous increase in the functional dissimilarity of co-occurring species (Heemsbergen et al., 2004). Although much debated, research in grasslands suggests that functional diversity is of greater importance than species richness for soil microbial biomass and activity (e.g., Ebeling et al., 2014), while there is even less conclusive information for forest ecosystems (Scherer-Lorenzen et al., 2007) using belowground traits (but see Guerrero-Ramírez et al., 2021). Unfortunately, access to and measurement of the above- and belowground traits on the same plants is often not possible for logistical reasons. To overcome this lack of data, phylogenetic diversity can be used as a proxy for functional diversity (Tucker et al., 2018), which has been used successfully for aboveground ecosystem functions (Cadotte et al., 2009).

Species richness levels	Plot size (m ²)	Number of plots	Minimum tree distance (m)	Tree density (trees/m ²)	References
1, 2, 3	From 45 to 196	80 [92]	1	1.0	http://www.treedivnet.ugent.be/ExpBanger.html
1, 2, 4, 8, 16, [24]	666.6	60 [566]	1.29	0.6	Bruehlheide et al. (2014)
4 (+FD)	1,700	24 [25]	1	0.7	Scherer-Lorenzen et al. (2007b)
1, 2, 3, 4	1,764	126 [127]	1.5	0.4	Verheyen et al. (2013)
1, 2, 6	14.4	187 [192]	0.4	8.2	Tobner et al. (2013)
1, 2, 6	14.4	190 [192]	0.4	8.2	Tobner et al. (2013)
1, 2, 3, 5, 6	25	96 [98]	0.8	1.2	Hantsch et al. (2014)
1, 2, 3, 4, 5	400	61 [256]	2	0.3	Castagneyrol et al. (2013)
1, [4,] 16	40,000	27 [124]	3	0.003	Hector et al. (2011)
1, 2, 5, 9, 18	2,025	46 [46]	3	0.1	Scherer-Lorenzen et al. (2007a)
1, 2, 3, 5	400	113 [163]	1.5	0.4	Vehviläinen and Koricheva (2006)
	3,937.5 ± 11,381.2	Total: 1,010	1.6 ± 0.9	1.1 ± 1.2	

Here, we present the first coordinated sampling and analysis of soil microbial properties across 11 tree diversity experiments distributed across four biomes. To explore potential effects of tree diversity on three key soil microbial properties (soil microbial basal respiration, biomass and carbon-use efficiency), we tested effects of tree species richness (the biodiversity measure most

frequently manipulated in tree diversity experiments; Verheyen et al., 2016) and tree phylogenetic diversity. We expected that phylogenetically diverse experimental forests would provide more dissimilar resources and niches to soil microorganisms, thereby increasing soil ecosystem functioning. We investigated the following three hypotheses. First, both tree species richness and phylogenetic

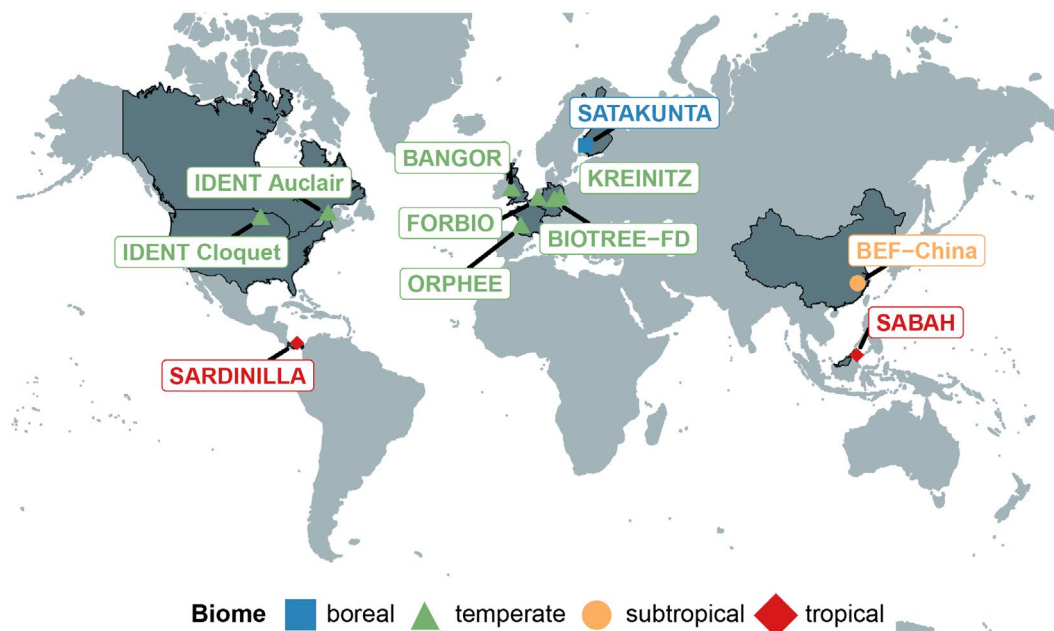


FIGURE 1 Locations of the 11 tree diversity experiments and assignments to biomes (Olsen et al., 2001). Details on the locations and experimental designs are shown in Table 1 [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.13461)]

diversity are predicted to increase soil microbial processes, but phylogenetic diversity is expected to have stronger effects. Second, abiotic drivers strongly influence soil microbial functions, because high soil C concentration, SWC and more neutral soil pH are hypothesized to increase the biomass, activity and carbon-use efficiency of soil microorganisms. Third, interactions among abiotic and biotic drivers might influence soil microbial properties, given the context dependence of biodiversity–ecosystem function relationships.

2 | MATERIALS AND METHODS

Soil samples were taken in 2013 from 11 tree diversity experiments that are part of the global network TreeDivNet (Verheyen et al., 2016; <http://www.treedivnet.ugent.be/>). The experiments are independent of each other, with different experimental designs and plot configurations (Table 1). Experiments are distributed across four continents (Asia, Europe and North and South America) and four different biomes (boreal, temperate, tropical and subtropical; Olson et al., 2001) and differ in age, with the youngest experiments running for 3 years and the oldest for 14 years as of 2013 (i.e., the year of the sampling campaign; Figure 1; Table 1). In total, 106 tree species were included in this study (Table S1). Experiments had a mean \pm SD of 3.7 ± 1.0 diversity levels, with diversity levels ranging from monocultures to 18 tree species in subtropical/tropical regions. All experiments had an experimental gradient in tree species richness, with the exception of one (BIOTREE-FD; see Table 1) that manipulated functional diversity at a constant level of tree species richness.

2.1 | Soil sampling

Soil samples were taken from a depth of 0–10 cm, excluding the litter layer, using a soil corer. Temperate and boreal experiments were sampled in the summer season in the Northern Hemisphere, whereas subtropical and tropical experiments were sampled in the wet summer season. All experiments were sampled between June and September 2013. Depending on the size of the experimental plot, different numbers of subsamples were taken per plot to create one composite sample. Three subsamples were taken for plots $<100 \text{ m}^2$, whereas 10 subsamples were taken for plots $>100 \text{ m}^2$. These subsamples were taken to capture the spatial heterogeneity of the plot and to represent as many different combinations of tree species as possible. Soil samples were always taken in the centre of surrounding tree stems. Immediately after sampling, soil samples were stored at 5°C until sieving at 2 mm and then were stored at -20°C until and during shipping to minimize changes in microbial activity, biomass and composition. Alternatively, if shipping at -20°C was not possible, samples were defrosted during shipping and were measured shortly after arrival. Altogether, 1,010 plots were sampled across the 11 tree diversity experiments (Table 1).

2.2 | Measurement of soil microbial properties

Before the start of microbial measurements, samples were kept at $+20^\circ\text{C}$ for 5 days to unfreeze and to adapt the soil microbial community to a constant and standardized temperature. Three different soil microbial community properties were assessed using an automated O_2 microcompensation system (Scheu, 1992).

First, basal respiration (in microlitres of oxygen per hour per gram of dry soil) was measured as the mean oxygen consumption per hour without the addition of any substrate. The mean oxygen consumption was measured for hours 15–20. Basal respiration reflects the active part of the soil microbial community at the time of sampling.

Second, microbial biomass carbon was measured by substrate-induced respiration (i.e., the respiratory response of microorganisms to addition of glucose and water). To saturate catabolic microbial enzymes, 8 mg glucose/g soil dry weight was added as an aqueous solution to the soil samples. The lowest substrate-induced respiration of three contiguous hours within the first 10 h was taken as the maximum initial respiratory response (MIRR; a period when microbial growth has not started). Microbial biomass (in micrograms of carbon per gram of dry soil) was calculated as $38 \times \text{MIRR}$ (in microlitres of oxygen per hour per gram of dry soil) following Beck et al. (1997). By providing water and glucose, the maximum potential of the living microbial biomass that is able to use glucose is activated, whereas for basal respiration only a fraction of the entire community is active.

Third, the microbial-specific respiratory quotient (in microlitres of oxygen per milligram of microbial carbon per hour) was calculated as the ratio of basal respiration and soil microbial biomass. The specific respiratory quotient is a measure of soil microbial carbon-use efficiency. Carbon-use efficiency is high when microbial biomass can be built up without high investment in basal respiration, which is indicated by a lower specific respiratory quotient. All measurements were conducted at $+20^\circ\text{C}$ in an air-conditioned laboratory using the same analytical devices (RMS Schuller, Darmstadt, Germany).

2.3 | Diversity metrics

In addition to tree species richness, we aimed at testing a tree diversity metric that captures the functional diversity of each experimental forest plot. However, comparable trait measurements were not available from all experiments or from the TRY database. Instead, we used phylogenetic diversity as a proxy for multitrait functional diversity (Tucker et al., 2018). Phylogenetic diversity indices have been shown to be powerful predictors of biodiversity–ecosystem functioning relationships (e.g., Craven et al., 2018) and are suggested to work when key functional traits are not available (Paquette et al., 2015). We used the molecular phylogeny from previous studies (Pietsch et al., 2014; Zanne et al., 2014) as a backbone to build a phylogeny of all species within the tree diversity experiments, conservatively binding species into the backbone

using dating information from congeners in the tree. We used the *comparative.comm* function in the R package *pez* to calculate a set of phylogenetic diversity indices, specifically mean phylogenetic diversity (MPD), mean nearest taxonomic distance (MNTD) and the standardized version of both to account for correlation with species richness (Pearse et al., 2015). The MNTD was found to correlate less (using Pearson correlation) with the logarithm of species richness and, therefore, was used in all the following analyses (Table S2). Taxonomic names of tree species were standardized using the website <https://tnrs.biendata.org/>

2.4 | Soil characteristics

We included a set of explanatory variables to describe the experimental sites, which were shown to have an effect on soil microbial properties and reflect the designs and local conditions of the different experiments (Figure S1). Gravimetric SWC was measured as the percentage of H₂O from fresh soil weight by drying the whole sample at 75°C for 3 days. Soil pH and soil C (as a percentage) were measured at the block level to obtain information about soil quality characteristics of each experiment. Therefore, equal proportions of dry soil were weighed from each sample to form a composite sample. The whole sample was ground, and an aliquot of 10 g was used for pH measurements by adding 0.01 M CaCl₂. Soil C concentrations were analysed by using the ground soil with an elemental analyser (Vario EL Cube, Elementar). We also extracted clay (percentage), sand (percentage) and silt (percentage) content from the SoilGRIDS database (Hengl et al., 2014).

2.5 | Environmental conditions

For each experimental site, we extracted mean annual temperature (MAT), the seasonal variability of temperature (Season. Temp.), mean annual precipitation (MAP) and the seasonal variability of precipitation (Season. Prec.) from the WorldClim database (<http://www.worldclim.org/current>) with 2.5 arc-min resolution. Potential evapotranspiration (PET) and the aridity index (MAP/PET) were extracted from CGIAR-CSI (<https://srtm.csi.cgiar.org/>). In addition, we obtained the age of the experiment (in years) and tree density (number of trees per square metre) from publications associated with each experiment (Table 1) and the TreeDivNet website (<http://www.treedivnet.ugent.be/>). Biomes were assigned based on the work of Olson et al. (2001).

2.6 | Data analysis

Before analysis, all data were centred and standardized (i.e., rescaled to a variance of one) using the *scale* function from the base package in R, and the distributions of response variables were checked visually. We included abiotic variables in our linear mixed-effects models

only when block or plot-level data were available (i.e., SWC, soil pH and soil C), allowing us to test all possible two-way interactions. In addition, we included logarithmized tree species richness (log SR) and MNTD as fixed effects in our models. We tested whether our models were overfitted by calculating the variation inflation factor (VIF) for each model and simplifying them by removing interactions with VIF > 3 (Montgomery et al., 2012). Given that only one interaction of soil pH and soil C for basal respiration and the respiratory quotient showed a VIF between 3.0 and 3.6, we used model comparison with ANOVA to check the Akaike information criterion (AIC). Both models, the reduced and the full model, did not differ by more than two units. Therefore, the full models were retained and are presented here.

The random effect structure accounted for the hierarchical data structure, with block nested within site and site nested within experiment. The Kenward–Rogers approximation was used to test for the significance of fixed effects and degrees of freedom. Marginal and conditional R^2 were calculated using the function *rsquaredGLMM* from the *MuMIn* package. Marginal R^2 represents the variance explained by the fixed effects, whereas conditional R^2 represents the variance explained by both fixed and random effects. Collinearity among explanatory variables in mixed-effects models was below $r = |0.7|$, as suggested by Dormann et al. (2013) (Figure S1). We checked model assumptions of the most parsimonious models by fitting model residuals versus the results of fitted models. Basal respiration and the respiratory quotient were \log_{10} -transformed to achieve the requirements of parametric statistical tests. Model fits of the mixed-effects models were used to plot estimates using the function *plot_model* from the package *sjPlot*. Significant interactions were plotted using *ggpredict* from the package *ggeffects*.

Principal components analysis (PCA) was used to visualize how every single experiment was characterized by the explanatory variables and their relationship to the dependent variables. Basal respiration, microbial biomass and the respiratory quotient were treated as active variables in addition to the explanatory variables available. The PCA was computed using *prcomp* from the *stats* package. Visualization was done using the function *fviz_pca_biplot* from the *factoextra* package.

In addition to linear mixed-effects models and the PCA, we included a piecewise structural equation model (pSEM; Lefcheck, (2016)) to investigate causal relationships among variables because there is uncertainty about underlying mechanisms (Figure S2; Table S4). The pSEM also allowed us to account for the nested structure of the underlying data. We accounted for correlated errors of all microbial properties, in addition to tree species richness and MNTD. Owing to the mismatch in data resolution, we could not test some potential effect pathways. For instance, we were unable to test whether increasing sand content reduced soil C content, which, in turn, was negatively related to SWC, in turn, was positively related to soil microbial properties but with an overall negative effect on soil microbial biomass. Independent claims were all non-significant. All variables were scaled as mentioned above. All statistical analyses were performed in R (v.4.0.3) (R Core Team, 2016).

3 | RESULTS

Mean soil basal respiration (\pm SD) was $2.06 \pm 1.94 \mu\text{O}_2/\text{h/g}$ soil dry weight, with the lowest values in the FORBIO experiment in Belgium (minimum: $0.08 \mu\text{O}_2/\text{hr/g}$ soil dry weight) and the highest values in the SATAKUNTA experiment in Finland (maximum: $15.26 \mu\text{O}_2/\text{h/g}$ soil dry weight; Supporting Information Appendix S4: Figure S4.3). Likewise, we found the lowest soil microbial biomass values in the FORBIO experiment (minimum: $11.85 \mu\text{g}$ microbial C/g soil dry weight) and the highest values in the SATAKUNTA experiment (maximum: $2501.54 \mu\text{g}$ microbial C/g soil dry weight). Mean soil microbial biomass was $435.51 \pm 325.03 \mu\text{g}$ microbial C/g soil dry weight. The respiratory quotient was lowest (i.e., highest carbon-use efficiency) in the BIOTREE-FD in Germany (minimum: $0.008 \mu\text{O}_2/\mu\text{g}$ microbial C/h) and the highest respiratory quotient was measured in the ORPHEE experiment in France (maximum: $0.0395 \mu\text{O}_2/\mu\text{g}$ microbial C/h). The grand mean across experiments for the respiratory quotient was $0.0052 \pm 0.0031 \mu\text{O}_2/\mu\text{g}$ microbial C/h. Mean SWC was $17.2 \pm 11.5\%$, and the driest soil was found in the IDENT Cloquet experiment in Minnesota, USA (minimum: $<0.1\%$), whereas the highest values were measured in the experiment SATAKUNTA (maximum: 58.5%).

Principal components analysis highlighted the strong relationship of basal respiration and microbial biomass to SWC, experimental

age and soil C that exhibited the strongest correlation with the first PCA axis and explained 59.3% of the variance (Figure 2; Table S3). These three variables reached maximum values in the boreal experiment SATAKUNTA. The high microbial biomass values found in the Biotree-FD experiment could be linked to higher clay content and lower potential evapotranspiration. The second axis explained 36.2% of the variance and was mainly affected by the seasonality of temperature, soil pH and tree density, which are variables that strongly increased the carbon-use efficiency.

3.1 | Hypothesis 1: Tree diversity increases soil microbial properties

Overall, tree species diversity and phylogenetic tree diversity did not significantly influence basal respiration, microbial biomass or carbon-use efficiency (Figure 3; Table 2). Likewise, a detailed examination of each experimental forest revealed only one positive significant effect, which was found in the ORPHEE experiment, where carbon-use efficiency increased (i.e., the respiratory quotient decreased) with increasing MNTD (Figure S3f; Table S5), whereas the other two significant effects showed negative relationships (Sardinilla: Figure S3a; and BEF-China: Figure S3e; Table S5). Consequently, the R^2 of the

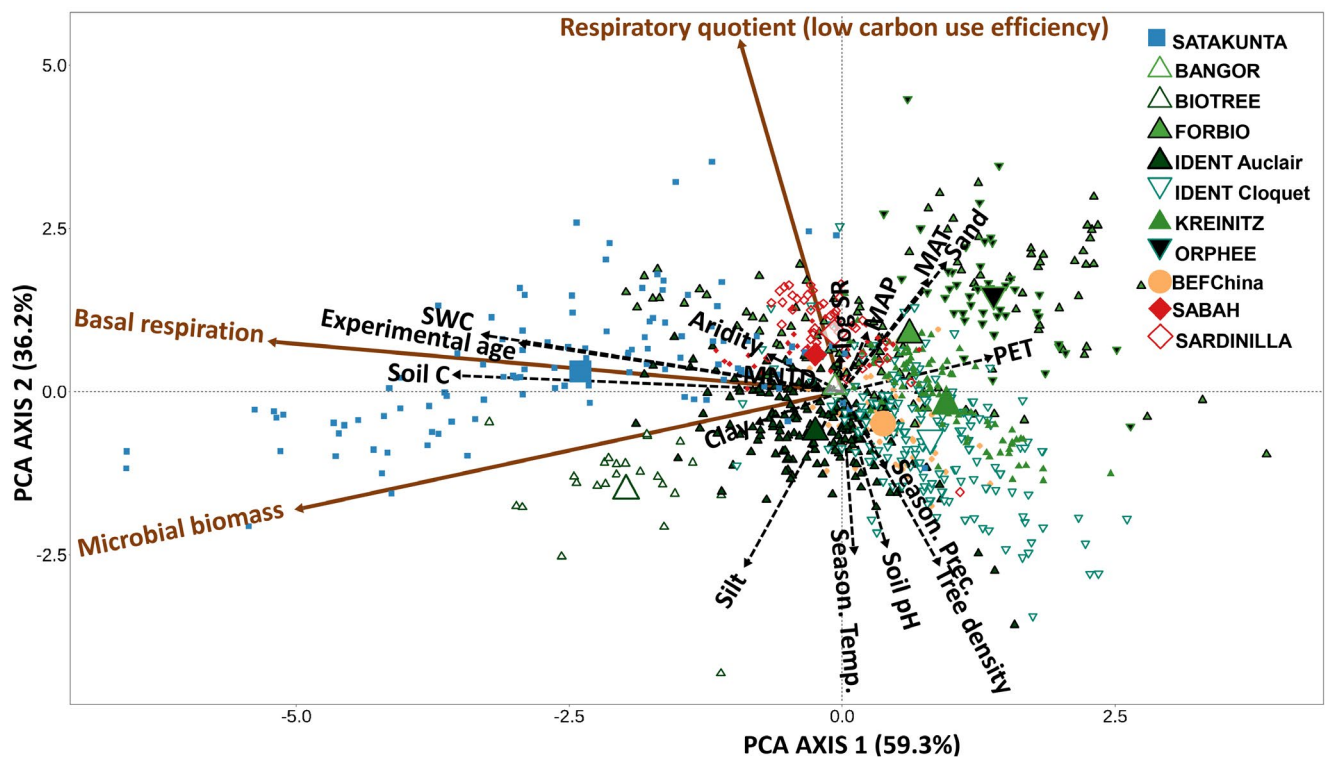


FIGURE 2 Principal components analysis (PCA) with the three microbial properties in focus (given in brown; basal respiration, microbial biomass and the respiratory quotient), in addition to the abiotic variables soil water content (SWC), soil carbon (C), sand, silt, clay, seasonality of temperature (Season. Temp.) and precipitation (Season. Prec.), soil pH, potential evapotranspiration (PET), mean annual temperature (MAT), mean annual precipitation (MAP) and aridity, and the biotic variables experimental age, tree density, tree species richness (log SR) and mean nearest taxonomic distance (MNTD), in 11 tree diversity experiments in boreal (blue; $n = 1$), temperate (green; $n = 7$), subtropical (yellow; $n = 1$) and tropical (red; $n = 2$) biomes. All variables were scaled. Percentage values in parentheses give the variance explained by the different PCA axes. Large symbols represent the centroids of the samples for each experiment. Correlations between moderators and the principal components can be found in the Supporting Information (Table S3)[Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

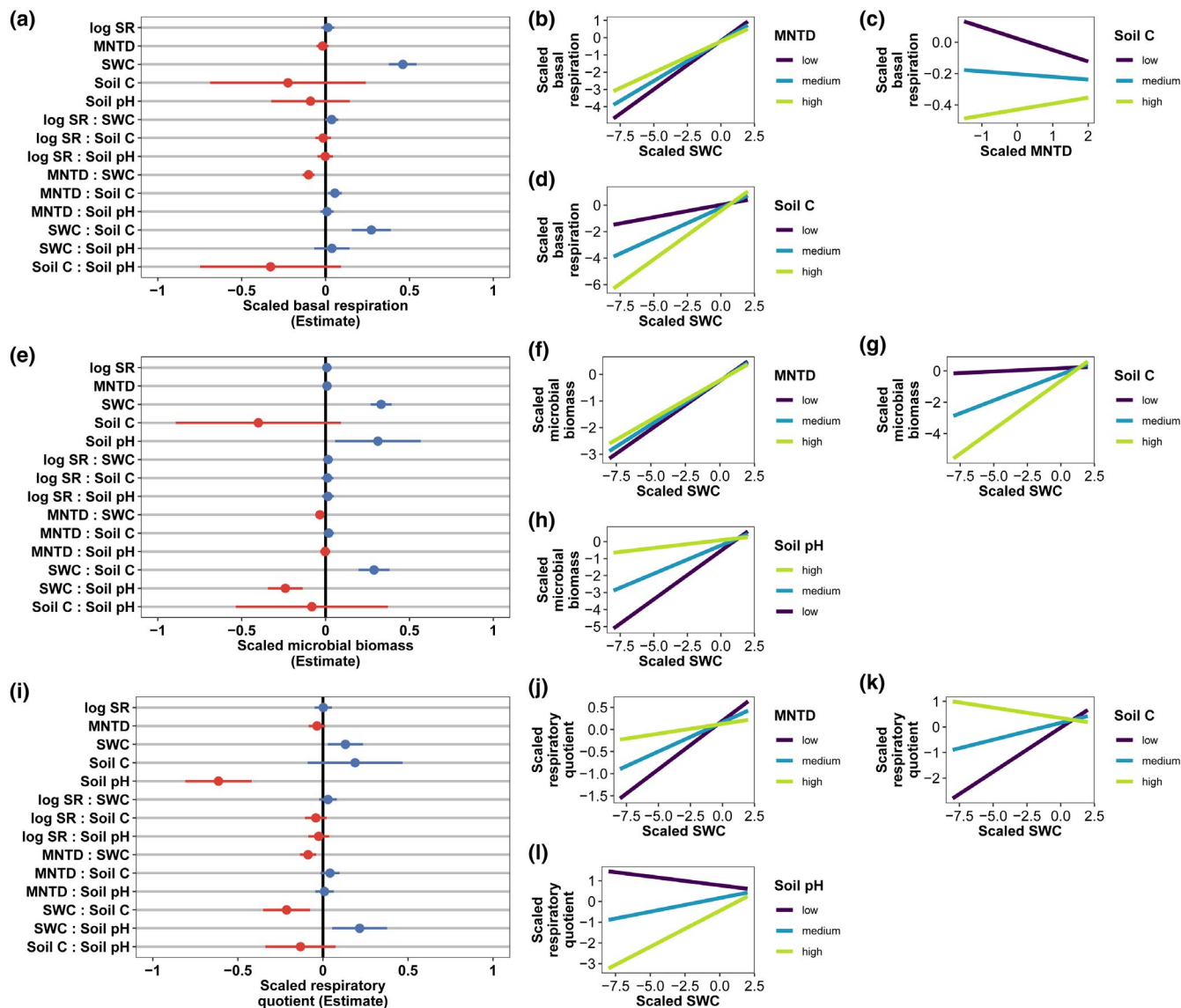


FIGURE 3 Coefficient estimates of linear mixed-effects models for three soil microbial properties (basal respiration, microbial biomass and the respiratory quotient) as affected by two tree diversity metrics, namely tree species richness (log SR) and mean nearest taxonomic distance (MNTD), and abiotic variables affecting soil microbial properties the most [i.e., soil water content (SWC), soil carbon (C) and soil pH]. Blue indicates a positive effect of the fixed factor on the response variable, whereas red indicates a negative effect. For significant interactions (not crossing the zero line), interaction plots are given as smaller panels, where one of the variables was categorized into low, medium and high levels. [Colour figure can be viewed at wileyonlinelibrary.com]

models analysing individual experimental forests were consistently low (Table S5), indicating that soil microbial properties are not well explained by tree diversity. Across all experimental forests, marginal R^2 of the linear mixed-effects models were 17% for basal respiration and microbial biomass and 38% for the respiratory quotient (Table 3). Conditional R^2 was roughly twice as high as marginal R^2 .

3.2 | Hypothesis 2: High soil water content, soil C content and soil pH increase soil microbial properties

Soil water content increased all microbial properties significantly when all the experiments were considered together (Figure 2;

Table 2); this positive effect was seen in all but one (ORPHEE) experimental site (Figure S4a). In contrast, soil C alone did not affect any of the microbial properties investigated in the linear mixed models or in the pSEM (Figure 2; Table 2; Figure S2; Table S4). Interestingly, the relationship between soil C, soil respiration, microbial biomass and carbon-use efficiency was not positive as expected, but negative for many of the experiments, as mentioned above (Supporting Information Appendix S4: Figure S4.5). However, the very high C values in the boreal Satakunta experiment led to a generally positive effect that was removed in the linear mixed-effects models. Higher soil pH significantly increased microbial biomass and carbon-use efficiency (i.e., a negative effect on the respiratory quotient) but not basal respiration (Figure 3h,i).

TABLE 2 ANOVA table of linear mixed effects models testing the effect of biotic and abiotic factors on three microbial properties in 11 tree diversity experiments

Fixed factor	NumDF	Basal respiration			Microbial biomass			Metabolic quotient		
		DenDF	F	p	DenDF	F	p	DenDF	F	p
Scaled log SR	1	950.92	0.49	.485	946.76	0.28	.594	855.34	0.01	.937
Scaled MNTD	1	948.32	0.96	.328	944.48	0.41	.521	964.10	2.02	.156
Scaled log SWC	1	897.22	120.46	<.001	969.62	108.42	<.001	328.67	6.26	.013
Scaled soil C	1	20.55	0.90	.354	24.12	2.54	.124	6.49	1.76	.230
Scaled soil pH	1	18.05	0.56	.464	43.15	5.76	.021	14.79	38.00	<.001
Scaled log SR : scaled log SWC	1	954.09	3.37	.067	948.70	0.96	.327	714.17	1.24	.265
Scaled log SR : scaled soil C	1	945.70	0.36	.550	945.07	0.40	.526	956.39	1.66	.198
Scaled log SR : scaled soil pH	1	968.33	0.01	.936	965.28	0.61	.435	653.79	0.63	.426
Scaled MNTD : scaled log SWC	1	957.07	31.44	<.001	951.79	6.16	.013	963.34	12.93	<.001
Scaled MNTD : scaled soil C	1	949.95	7.04	.008	945.72	1.49	.223	961.91	2.17	.141
Scaled MNTD : scaled soil pH	1	953.69	0.19	.663	951.73	0.02	.891	960.43	0.11	.740
Scaled log SWC : scaled soil C	1	780.09	21.30	<.001	819.94	37.87	<.001	129.03	9.27	.003
Scaled log SWC : scaled soil pH	1	916.36	0.50	.481	889.17	20.53	<.001	90.30	6.85	.010
Scaled soil C : scaled soil pH	1	14.98	2.34	.147	16.70	0.12	.729	2.97	1.57	.300

Note: All variables were scaled. Significant effects ($p < .05$) are highlighted in bold.

Abbreviations: DenDF: denominator degrees of freedom; MNTD: mean nearest taxonomic distance; NumDF: numerator degrees of freedom; SR: tree species richness; SWC: soil water content.

TABLE 3 Akaike information criterion corrected for small sample size (AICc) and R^2 for mixed-effects models for three microbial properties as affected by tree diversity and abiotic factors in 11 tree diversity experiments

Response variable	d.f.	AICc	R^2 fixed (marginal)	R^2 random (conditional)
Basal respiration	19	1522.34	.33	.78
Microbial biomass	19	979.26	.17	.90
Respiratory quotient	19	2065.99	.38	.69

3.3 | Hypothesis 3: Context dependence

Although all three microbial properties were not affected by tree diversity itself, there was a significant effect of the interaction of MNTD and SWC on all three properties, and basal respiration was also affected by the effect of interaction of MNTD and soil C. The interactive effects of tree species richness with abiotic factors were, however, not statistically significant (Figure 3; Table 2). Generally, all soil microbial properties increased with increasing SWC. At low SWC, we detected significant positive effects of MNTD on soil microbial properties. In contrast, the effects of MNTD were not statistically significant at high levels of SWC (Figure 3b,f,j). High MNTD increased basal respiration and microbial biomass at low levels of SWC but decreased carbon-use efficiency.

The significant interaction effect of MNTD and soil C for basal respiration showed a different pattern. Generally, the fitted model predicted basal respiration to be highest when soil C was low (Figure 3c). Increasing MNTD increased basal respiration only at high soil C levels, whereas increasing MNTD decreased basal respiration at low soil C levels.

In addition to interactions with MNTD, we found additional interactions between the abiotic variables. A significant interaction

for all three microbial properties was found for soil C and SWC. At high SWC, differences in soil C had less impact on all soil microbial properties (Figure 3d,g,k). The increase in basal respiration and microbial biomass along the soil water gradient was steepest when soil C was high, and the reverse was true for the respiratory quotient.

Microbial biomass and carbon-use efficiency were significantly affected by the interaction of soil pH and SWC (Figure 3h,l). Effects of soil pH on soil microbial properties were negligible when SWC was high.

4 | DISCUSSION

Leveraging a global network of experimental forests, we found that variation in soil microbial properties was mediated by abiotic factors to a greater extent than by biotic factors. Effects of tree diversity on soil microbial respiration were largely context dependent, emerging only when SWC was low.

Our first hypothesis posited that, independent of environmental context, taxonomic and phylogenetic diversity would increase soil microbial properties. Yet, we found that tree diversity did not have statistically significant effects on any soil microbial property. Recent

studies in experimental plots found weak effects of tree diversity on soil microorganisms, suggesting that tree species identity might be a more important driver of soil microorganisms and soil functions (e.g., Gottschall et al., 2019; Khelifa et al., 2017). Individual tree species can affect the structure of the litter layer by influencing microclimatic conditions that drive soil microbial functions (Gottschall et al., 2019). Therefore, improved data on litter and root traits, in addition to their influence on soil quality and microclimate, are needed to improve our mechanistic understanding of the effects of tree identity on soil functions (Beugnon et al., 2021; Laliberté, 2017). Using belowground traits, rather than aboveground traits, is essential to predict soil functions, because different mechanisms are likely to operate belowground.

Unfortunately, no representative above- or belowground trait data were available for the 11 tree diversity experiments to investigate the effects of tree identity in greater detail. We were not able to use data from trait databases, because relevant traits were not available for many subtropical and tropical tree species. Instead, we used phylogenetic diversity (MNTD) as a proxy for differences among tree species (Craven et al., 2018). A notable drawback of using MNTD (or any other measure of phylogenetic diversity) is that it lacks a clear mechanistic link to soil microbial properties, nor can it be used to explore mechanistic identity effects. A targeted trait approach paired with phylogenetic information might help us to gain a better understanding of the underlying mechanisms. The growing network of global tree diversity experiments (Verheyen et al., 2016) and trait syntheses (Guerrero-Ramírez et al., 2021) will allow for coordinated approaches and should aim to measure belowground traits directly to identify abiotic and biotic drivers of soil microbial functions.

We did not find any interactive effects of tree species richness and abiotic factors on soil microbial properties, confirming that tree species richness per se does not necessarily influence belowground ecosystem functions (Guerrero-Ramírez et al., 2016) and/or that tree species richness did not interact with abiotic factors. Using phylogenetic diversity instead of tree species richness provided the advantage of having a more even data distribution. This is because the temperate and boreal experiments did not contribute to medium and high levels of tree species richness, whereas the limited number of tropical and subtropical experiments had higher levels of tree species diversity. The species pool of the sub- and tropical experimental forests had a more constrained phylogeny than that of the temperate experimental forests, possibly reflecting the absence of coniferous species and including multiple species of the same genera (Supporting Information Appendix S1: Table S1.1). This might explain the weaker (or more variable) effects of MNTD in tropical experimental forests than in temperate or boreal experimental forests.

Our study confirmed that soil microorganisms are mainly influenced by abiotic drivers (hypothesis 2), which were also important in modulating the effects of tree diversity (hypothesis 3). Soil water content was the dominant abiotic driver, affecting all soil microbial functions and interacting significantly with all mentioned abiotic drivers. The strong impact of SWC on soil microbial properties has

been shown in many studies (see the review by Schimel, 2018) and could be more important than nutrient availability (Singh et al., 2009). We found that at high SWC, changes in soil pH and soil C had minimal effects on the overall high values of soil microbial properties. For instance, positive effects of high temperature on soil biological activity can be achieved only when soil water is not limiting (Thakur et al., 2018), and nutrient availability can be increased by higher soil moisture via increasing diffusion of soluble organic substrates (Schimel, 2018). This suggests that optimal soil water availability (i.e., between 50 and 70% of the field capacity; Manzoni et al. (2012)) can mitigate the unfavourable effects of other abiotic factors on soil ecosystem functioning. For a better mechanistic understanding, microclimatic parameters (e.g., soil humidity and temperature) should also be included, which can provide new insights (Gottschall et al., 2019). Therefore, to maintain soil ecosystem functioning, especially when faced with more frequent dry periods owing to global change, tree species or communities might be selected that directly use water more efficiently, have a higher diversity in hydraulic traits (Anderegg et al., 2018) and/or have traits that indirectly maintain higher soil water levels (e.g., via higher leaf area, denser canopies or leaf litter traits that build a thick litter layer; Gottschall et al., 2019). In addition, further management practices (e.g., leaving leaf litter on the ground, applying mulch or planting a cover crop) might be needed to enhance SWC, and thus, to increase soil functioning.

The present study showed that the effects of tree diversity, as captured by phylogenetic diversity, on soil microbial properties were statistically significant at low soil moisture levels, confirming earlier findings of an observational study across European forests (Ratcliffe et al., 2017). In contrast, a recent study investigating the interaction with water availability and tree diversity on similar microbial properties did not find positive effects of diversity at low soil water availability (Strukelj et al., 2021); however, these authors investigated context dependence at only two experimental sites. Using 11 tree diversity studies, our findings suggest that biodiversity might function as a buffer against harsh environmental conditions and maintain ecosystem functioning under drought. As plant diversity increases soil microbial diversity, diverse soil microbial communities can increase the resilience of plants after drought (Prudent et al., 2020). For instance, biodiversity might enhance drought resistance owing to strengthened biotic interactions, for instance, via mycorrhiza (van der Heijden et al., 2008), especially when mycorrhization rates increase with increased tree diversity (Ferlian et al., 2021). Including microclimatic information would further help us to understand the underlying mechanisms, as shown by Gottschall et al. (2019), who found that higher night temperature associated with a specific tree species increased wood decomposition.

One mechanism by which tree diversity increases soil microbial properties is via enhanced inputs of soil C, because microorganisms are generally C limited (Soong et al., 2020). A recent global study investigating the effect of plant diversity (including 92 forest sites) on C stocks and microbial biomass C found significantly higher soil organic C in mixtures compared with monocultures but did not detect a generally positive effect of increasing species diversity on soil

C stocks and microbial biomass C (Chen et al., 2020). In the aforementioned study, C stocks increased with time, suggesting that more time is needed for effects of tree diversity to increase C stocks and likely cascading effects on microbial functions. Therefore, the lack of a consistent effect of diversity on soil C in the present study could be attributable to the young age of most experimental forests (average 7.2 ± 3.9 years). This also suggests that belowground responses to tree diversity might take much longer than aboveground responses (Guerrero-Ramírez et al., 2017).

Our dataset did not allow testing for three-way interactions, but the PCA together with the interactions of soil water suggest that high amounts of soil C and soil water increase soil microbial respiration and biomass the most. These two variables are strongly affected by soil texture at one experimental site (Guenet et al., 2011) but can also be affected by tree diversity, probably over the long term. We were not able to include soil texture data in our linear-mixed effects models, although other studies found strong effects (Xu et al., 2017). A statistical analysis (not presented) showed no effect of soil texture, probably reflecting the limited number of experimental sites and the data source (SoilGRID database; Hengl et al., 2014). Consequently, the benefits of afforestation efforts in terms of soil ecosystem functioning will not be immediate and will probably take more than a decade to manifest. However, planting trees with specific traits combined with targeted management practices might promote this effect.

4.1 | Conclusion

Global analyses of biodiversity–ecosystem functioning relationships aim to identify general patterns, context dependencies and underlying mechanisms to predict and mitigate the consequences of biodiversity loss for human well-being. Our results indicate that the effects of tree diversity on soil microbial biomass and respiration in young plantations are generally weak but are strongest in dry soil conditions. Notably, the results of tree diversity experiments can have important practical implications, because many degraded ecosystems are in the process of being reforested, and recommendations regarding how to enhance the multifunctionality of these restored ecosystems are urgently needed to mitigate climate change. Given that the potential impacts of high-diversity reforestation efforts will be likely to manifest over the long term, especially with regard to soil ecosystem functioning, we recommend management practices that maintain SWC. Doing so will require addressing key gaps in biodiversity data, particularly belowground functional traits. Exploring interactions between abiotic and biotic factors in driving soil microbial properties and carbon storage in future studies is pivotal in order to obtain a more mechanistic understanding of the driving forces of and management options for soil carbon storage.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at: <https://datadryad.org/stash/share/1jo89ZCsSXdGLlvO79rDRxPvB5DPe1n1zP6JBI83tP8>

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BIOSKETCH

The research team is part of TreeDivNet, which is a large network of tree diversity experiments investigating how different facets of tree diversity affect ecosystem functioning in major forest types around the world (<http://www.treedivnet.ugent.be/>).

SUPPORTING INFORMATION

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