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Research article

Leaf trait variation within individuals mediates the relationship between tree species richness and productivity

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In forest ecosystems, many ecosystem functions such as tree growth are affected by tree species richness. This biodiversity–productivity relationship (BPR) is mediated by leaf traits, which themselves are known to be influenced by tree species richness; at the same time, as the primary organs of light capture, they are an important factor for tree growth. However, how tree growth is influenced by a tree's ability to phenotypically adjust its leaf traits to the within-individual light gradient has largely been unexplored. Furthermore, it is not known how such impacts of within-tree leaf trait variation on individual tree growth sums up to productivity at the community scale. In this study we tested how tree species richness, a tree's mean leaf traits, within-tree leaf trait variation and the light extinction coefficient within a tree crown influence tree growth. We measured these variables in the temperate forest plantation of the Kreinitz biodiversity experiment. We found that the relationship between tree species richness and tree growth is mediated via the leaf trait variation of the individual trees, which in turn was modified by light availability. In particular, trees in monocultures show a higher within-individual leaf trait variation, which partly compensates for the lack in among-species leaf trait variation, and thus affects the BPR. It seems that tree richness operates both through increased acquisitive trait values and within-individual leaf trait variation, two processes that cancelled out each other and resulted in the absence of a significant effect of tree richness on productivity in our study. In conclusion, to understand the BPR, it is important to study the underlying processes and to know which ones reinforce or oppose each other. In particular, our study highlights the importance of including within-individual leaf trait variation in ecological research as one important moderator in the BPR.

Keywords: biodiversity-ecosystem-functioning experiment, diversity-productivity relationship, leaf traits, light availability, near-infrared spectroscopy (NIRS), temperate forest plantation



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Introduction

The diversity–productivity relationship in forest ecosystems

In ecological research, the relationship between tree species richness and productivity of forest ecosystems biodiversity–productivity relationship (BPR) has been intensively studied. While the driving mechanisms are still poorly understood, current research suggests a generally positive BPR (Chisholm and Gupta 2023). For natural forests, literature indicates a positive BPR (Zhang et al. 2012, Ruiz-Benito et al. 2014, Liang et al. 2016), especially when control for biome, climate and environmental conditions is applied (Paquette and Messier 2011, van der Plas 2019, Ratcliffe et al. 2017).

In planted biodiversity–ecosystem–functioning experiments, however, the pattern is less clear (Kambach et al. 2019). While there are multiple studies that reported a positive BPR in planted forests (Potvin and Gotelli 2008, Huang et al. 2018, Zemp et al. 2019), some studies described a negative (Firn et al. 2007) or no significant BPR (Nguyen et al. 2012, Staples et al. 2019). These divergent findings highlight that, in addition to a direct effect of biodiversity on productivity, indirect effects may determine the outcome of a BPR.

In general, there are multiple possible mechanisms that connect species richness and tree productivity (Ammer 2019, Trogisch et al. 2021). For example, in species-rich environments, higher tree growth might be related to stronger facilitation effects among species (Hooper et al. 2005) as well as to weaker effects of species-specific pathogens (Maron et al. 2011, Schnitzer et al. 2011). Furthermore, selection effects can cause positive BPRs (Tatsumi 2020). Selection effects might occur when well-performing species become more abundant in mixtures. Additionally, the biodiversity of primary producers in a community reduces the competition among them through niche partitioning (Tilman 1977). Competition is most severe for plants that are similar regarding their resource requirements and uptake strategy, which is in particular the case for plants of the same species (MacArthur and Levins 1967). Consequently, an increased biodiversity can lead to reduced competition for resources (Tilman 1994), and therefore to increased resource availability for each individual plant. This in turn results in increased productivity of the community (Fichtner et al. 2018).

Competition for light and optimisation of light capturing

In closed canopy forests, light is the resource that trees most compete for (Oliver and Larson 1996, Kohyama et al. 2012, Rüger et al. 2012). Hence, forest canopies are optimized for light capture (Reich 2012). In particular, a higher structural complexity appears to be linked to greater photosynthetic capacity of the forest (Seidel and Ammer 2023). Optimization for light capture occurs at all organisation levels of the community. There are differences between species in light demand and shade tolerance, differences between

individuals of the same species and even differences in the adjustment of leaves to light conditions within a single tree (Lichtenthaler et al. 1981, Givnish 1988, Bassow and Bazzaz 1997, Valladares and Niinemets 2008). A highly diverse forest should be more effective in partitioning the available light than a monoculture (Morin et al. 2011). Hence, diverse tree communities should be more productive than monocultures (Williams et al. 2021).

Leaf traits

The amount of light captured by an individual tree is dependent on the total leaf mass (Galia Selaya et al. 2008) and its leaf traits (Terashima and Hikosaka 1995). Numerous leaf traits are related to photosynthesis and light capture, including specific leaf area (SLA) and the concentration of nitrogen (leaf N) (Evans and Poorter 2001), calcium (leaf Ca) (Wang et al. 2019), potassium (leaf K) (Leigh and Wyn Jones 1984), magnesium (leaf Mg) (Shaul 2002) and phosphate (leaf P) (Plaxton and Carswell 1999) in the leaves. However, when analysing leaf traits, the optimisation of light capture also involves the tradeoff between these photosynthesis-related traits and the construction cost of the leaves (Zhang et al. 2017). Therefore, relevant traits also include leaf dry matter content (LDMC), leaf carbon content (leaf C) and ratio of leaf carbon to leaf nitrogen (CN ratio). On the species level, this tradeoff is described by the leaf economics spectrum (LES) (Wright et al. 2004). Traits related to the LES allow ranking plant species along the fast–slow growth spectrum according to their acquisitive or conservative strategy, with photosynthesis-related traits associated with an acquisitive strategy and structural traits associated with a conservative strategy (Reich 2014). Indeed, several studies clearly demonstrated the link between acquisitive leaf traits and fast tree growth (Poorter and Bongers 2006, Chaturvedi et al. 2011, Li et al. 2017).

Leaf trait variation

Leaf traits of the LES have been traditionally considered at the species level (Garnier et al. 2001, Díaz et al. 2016). However, mean trait values may fail to predict tree growth (Paine et al. 2015) which is why, in addition to the average leaf trait values of a species, the ability of a species to adjust its leaf traits (leaf trait variation) has also been linked to tree growth (Laforest-Lapointe et al. 2014, Lusk 2019, Asefa et al. 2021). Indeed, the topic of intraspecific leaf trait variation has received much attention in recent years (Albert et al. 2010, Messier et al. 2010, Violle et al. 2012). The link between intraspecific leaf trait variation and tree growth has been described in the context of the ability of a species to adjust its leaf traits to environmental gradients (Hikosaka et al. 2021, Kühn et al. 2021, O'Sullivan et al. 2022). Furthermore, leaf trait adjustments on smaller scales might be also relevant, albeit as responses to different factors. For forest ecosystems, the leaf trait variation within individual trees (within-individual leaf trait variation) could be especially relevant, as here every tree is subject to a

strong within-individual light gradient (Binkley et al. 2013). Plants respond to the within-individual light gradient with leaf trait value adjustments at the within-individual level (de Kroon et al. 2005, Kawamura 2010). The consequence is a strong individual leaf trait variation in tree crowns (Chmura and Tjoelker 2008). Irrespective of a species' position on the LES spectrum, it would be beneficial to adjust the leaf traits to the sun–shade gradient along the crown, thus making best use of the given light conditions by making sun and shade leaves. At the level of individual trees, this ability of leaf trait adjustment would be seen in an increased leaf trait variation. Yet, studies that link individual leaf trait variation to tree growth are rare (Feng et al. 2022 studied the vertical variation in leaf traits to understand the coexistence of tree species).

A major hurdle for such analyses is the high effort of analysing the required amount of samples. A possible solution is the use of near-infrared spectroscopy (NIRS) in ecological research (Trogisch et al. 2017), as it offers a rapid and effective method for the analysis of leaf traits (Foley et al. 1998).

In this study, we investigated whether a higher individual trait variation allows an individual tree to better adjust to the within-individual light gradient in order to optimise its light capture. We analysed a wide arrange of leaf traits with a focus on those related to the LES. While the LES is a framework that describes between-species trait correlation, there is a strong indication that it can be extended to the trait coordination within tree canopies (Niinemets et al. 2015). Thus, we applied the LES concept to within-individual trait values.

Aim and hypotheses

The aim of this study is to identify the key underlying mechanism of the BPR in a temperate forest ecosystem. In the Kreinitz tree diversity experiment (Saxony, Germany), we analysed the growth of all 2880 trees over a three-year period. For a subset of 283 individuals we measured leaf traits, leaf trait variation and the light extinction coefficient at the within-individual level. We predicted a generally positive relationship between tree species richness and tree growth (H1). We expected to find this relationship both at the plot level (H1a) and at the individual level (H1b). While H1a tests for a positive net biodiversity effect on tree growth, H1b assumes that tree richness has a positive effect on growth of the majority of tree species. Moreover, we expected that tree-level mean trait values of the LES and within-individual trait variation are driven by tree species richness (H2a) and a tree's light extinction coefficient (H2b). Furthermore, we hypothesized that individual tree growth depends on leaf traits (H3), and trees grow better with a more acquisitive mean LES trait value (H3a) and a higher LES trait variation (H3b). Finally, we expected that mean trait values and trait variation are mediating factors of how tree species richness affects tree growth (H4a). We also tested whether the way light is intercepted along the crown mediates the relationship of tree species richness with mean trait values and trait variation (H4b). The mediating effects in H4 were tested with a structural

equation model (SEM) (see the Supporting information for the tested relationships within the model).

Material and methods

Experimental site

The Kreinitz experiment is located in central Germany near the city of Riesa, Saxony (51°23'08"N, 13°15'41"E). The experimental site was established in 2005 on former agricultural land (humic cambisol) and is partially surrounded by pine forest. The experiment covers six common European tree species: European beech *Fagus sylvatica*, European ash *Fraxinus excelsior*, Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, sessile oak *Quercus petraea* and small-leaved linden *Tilia cordata*. The 2880 tree individuals are distributed over 98 plots in two blocks of 49 plots each (Supporting information). Each block consists of one plot each for all monocultures, one plot each for all possible two, three and five species mixtures, one plot for the six species mixture, as well as one control plot without trees. The position of the plots within blocks is random. The number of different tree species planted in a plot is referred to as 'tree species richness'. Each plot covers an area of 25 m², on which 30 individuals are planted in five rows of six individuals. The planting distance is 80 cm between individuals within rows and 100 cm between rows with a horizontal offset of 40 cm for every second row, which results in a hexagonal planting pattern. For further information on the Kreinitz experiment, see Hantsch et al. (2014).

Sampling

Biometry and leaf sampling

Tree height and basal area of all trees in the Kreinitz experiment were measured in winter 2013/2014 and winter 2016/2017. Woody biomass of the trees was calculated according to Annighöfer et al. (2016) using species-specific factors (Supporting information). Tree growth was calculated as the relative increase of the above-ground woody biomass between the two measurement periods. This method suggested negative growth values for six individuals. While negative growth is not implausible (Pastur et al. 2007), e.g. owing to die-back of the main stem and thus decline in tree height, we cannot rule out that this is a result of measurement errors. However, we decided not to remove these values from the dataset as suggested by Pastur et al. (2007) and Sheil et al. (2016), because in sum, negative and positive measurement errors can be assumed to cancel each other out. Therefore, selectively removing negative growth values might add a significant bias to the dataset (Sheil et al. 2016).

We applied multiple methods to calculate tree growth, in order to answer the question of how dead trees would influence plot level performance. The mortality rate of the trees does not necessarily correspond to the productivity of the forest, because even a high mortality might be compensated

for by increased growth of the surviving trees (Guerrero-Ramírez et al. 2017).

First, we calculated the ‘absolute growth on plot level’ expressed as increase of woody biomass in kg between the surveys. The absolute growth refers to the difference of the sum of the woody biomass of all trees of a plot that were alive during the particular survey. Thus, the trees that died between the surveys (140 out of 2660 individuals) were considered as part of the total woody biomass during the first but not the second survey.

Second, we calculated the ‘relative growth on plot level’ expressed as relative increase of woody biomass in relation to the first survey. The relative growth refers to the difference in the sum of the woody biomass of all trees of a plot divided by the woody biomass of the first survey. In this case, the woody biomass did not contain trees that were not alive during both surveys.

Finally, we calculated the ‘relative growth on individual level’ analogue to the calculation on the plot level. Here, the relative growth refers to the difference in woody biomass for each tree, divided by that tree’s woody biomass of the first survey. This calculation also did not include trees that were not alive during both surveys.

Leaf sampling took place in July/August 2017. A subset of 283 individuals (48 in monocultures, 83 in two species mixtures, 81 in three species mixtures, 59 in five species mixtures and 12 in six species mixtures) was selected for leaf sampling. For each tree, up to five sampling points were chosen, which were evenly distributed along the outer crown of the tree. At each sampling point up to eight fully developed leaves without visible damage were harvested (total sample size = 3656 leaves), sealed in moist plastic bags and stored cold until further analysis on the same day.

Light measurement

At each sampling point we took light measurements directly above the subsequently sampled leaves using an LI-1400 data logger in combination with a LI-190SA quantum sensor. As a reference, a second identical setup was placed outside of the experiment, exposed to the open sky. Light was measured as the photosynthetic active radiation (PAR; 400–700 nm) expressed in $\mu\text{mol s}^{-1} \text{m}^{-2}$. The relative light availability was calculated as the quotient of both values (PAR sampling point/PAR open sky). In each tree, the increase of relative light availability with measurement height was considered to follow the Lambert-Beer law (as demonstrated by Vose et al. (1995) or Kitajima et al. (2005)) and was therefore fitted as an exponential curve according to Eq. 1:

$$y = c \times a^x \quad (1)$$

where y is the relative light availability at the measuring point, c (the intercept of the fitted curve with the y -axis) is the relative light availability at the lowest part of the tree crown, x (the exponent of the fitted curve) is the relative height in the crown and a (the basis of the fitted curve) expresses the

slope of the light/height curve. The latter value describes the light distribution within the crown. The value of a should be higher in a scenario where a tree captures the majority of the available light in the top of the crown and low if the light interception is evenly distributed along the crown. We consider this value (i.e. the steepness of the light gradient) as an indicator for the light extinction coefficient of an individual tree. See the Supporting information for visualisation of the light curves.

Leaf trait analysis

We analysed all leaves for SLA, LDMC, CN ratio, leaf C, leaf N, leaf Mg, leaf Ca and leaf K as these leaf traits are related to photosynthesis or leaf structure, which allows a ranking on the acquisitive-conservative axis of the LES. Leaf traits were analysed via NIRS using an ASD FieldSpec 4 Wide-Res spectroradiometer. Each leaf was scanned threefold using a contact probe. The scans recorded relative reflectance values for each spectral region between 350 nm and 2500 nm. We selected a subset of 152 leaves for NIRS prediction model development and analysed them with conventional means (see the Supporting information for reference methods). We created individual prediction models for each leaf trait using R (ver. 4.0.3; www.r-project.org) and a modified version of the ‘plantspec’ package (ver. 1.0; Griffith et al. (2019)). Our modification included a further optimization of the calibration process, which aimed at improving prediction model accuracy at the cost of longer calculation time. In particular, we added a loop that repeatedly re-iterated randomly selected combinations of spectral bands and mathematical pre-treatments until the most precise prediction model was found (Proß 2023). We validated the prediction models via test-set validation using one-third of the samples (randomly drawn) as validation samples and two-thirds as calibration samples. The validation results indicate model accuracy (Supporting information). Subsequently, we applied the prediction models to all scans and averaged them at the leaf level to reduce instrument noise.

Statistical analysis

All statistical analyses were conducted using R (ver. 4.0.3; www.r-project.org). All linear mixed effects models were fitted by using the *lmer* function in the ‘lmerTest’ package (ver. 3.1-3; Kuznetsova et al. (2017)). These models were analysed using type three sum of squares in the analysis of variance with Satterthwaite approximation for degrees of freedom.

Growth as a function of tree species richness

We fitted two linear mixed effects models to assess the influence of tree species richness on plant growth at the plot level (H1a). The first model used the absolute increase in plot level woody biomass between the two surveys as response variable, and tree species richness as explanatory variable. The second model was fitted with the plot mean of the relative increase in woody biomass of each tree in a plot. Both models also contained the block and the species composition as nested

random factors. Thereby, the species composition accounts for different species combinations that have been established at a given level of tree species richness.

To assess the influence of tree species richness on plant growth at the individual tree level (H1b), the relative increase in woody biomass was calculated for each tree. A linear mixed effects model was fitted that contained the relative increase in woody biomass of every tree as response variable, and a numeric value for the tree species richness as a fixed effect. The model also accounted for the identity of the tree species as a random effect crossed with another nested random effect which consisted of block, species composition and plot, orthogonal to the first random effect. In addition, the same model was fitted for a subset of the trees, excluding all coniferous trees.

Within-individual coordination of leaf traits

We conducted a principal component analysis (PCA) using all measured leaf level traits. As this PCA was strongly affected by the differences in species mean values (Supporting information), we calculated a second PCA by centring the leaf level traits, which was achieved by subtracting the species mean value from each observed value of that species and dividing the result by the trait's SD of each species. For broadleaved trees, both PCAs captured the LES on the first axis (Results), and we used the scores for each leaf on the first PCA of the centred PCA axis as proxy for the position within the LES. To obtain trait values for the whole tree, all single leaf values were aggregated per tree using the arithmetic mean (hereafter, 'mean trait scores'). The trait variation of each individual tree was calculated as the SD of the trait value of every leaf of the tree's mean. However, for the coniferous trees, the PCA axes did not capture the LES, which is why we were unable to use an axis score as a proxy for the position within the LES, as well as its SD as proxy for the leaf trait variation. Consequently, we removed the conifers from the analyses that are based on these values.

Traits as a function of tree species richness and light extinction coefficient

To analyse the effect of tree species richness and the light extinction coefficient on mean trait scores and leaf trait variation, we fitted two separate linear mixed effects models, using either the mean values or the SD of the scores of leaf traits on the first PCA axis as response and both tree species richness and the light extinction coefficient as predictors. As above, both models included tree species identity as a random effect crossed with another nested random effect which consisted of block, species composition and plot. Both models were fitted without interactions to fully match the structure of the SEM (below). Furthermore, both models were calculated only with data from the four deciduous tree species, excluding the two coniferous species.

Influence of tree species richness, mean trait scores, leaf trait variation and the light extinction coefficient on individual tree productivity

To address whether individual tree productivity is dependent on tree species richness, the light extinction coefficient, mean trait scores or leaf trait variation, we fitted a linear mixed

effects model that included tree growth as response variable and all four fixed effects simultaneously. In contrast to the model fitted for H1b, only broadleaved trees were included for which traits were measured. This model had the same random structure as the mixed models described above and also did not include interactions.

Mean trait scores and leaf trait variation as mediators and light as a covariate for the BPR

A SEM was fitted using the 'piecewiseSEM' package (ver. 2.1.2; [Lefcheck and Freckleton \(2015\)](#)). The model contained broadleaved trees with tree species richness as an exogenous variable, and light extinction coefficient, mean trait scores, leaf trait variation and the relative tree growth at the individual level as endogenous variables (see the Supporting information for the path diagram and model description). Tree growth was explained by species richness, light extinction coefficient, mean trait scores and leaf trait variation; the leaf trait variation was explained by species richness, light extinction coefficient and mean trait scores; the mean trait scores were explained by species richness and light extinction coefficient; and finally, light extinction coefficient was explained by species richness. As in the models above, tree species identity as a random effect crossed with another nested random effect which consisted of block, species composition and plot. Additionally, separate SEMs were fitted for each species using the same model structure but omitting species identity as a random factor.

Results

Relationship of tree growth and tree species richness

The analysis of all trees of the Kreinitz experiment did not show any significant relationship between tree growth and tree species richness in the timeframe of three years. At the plot level, there was no relationship between tree species richness and tree growth, neither with respect to absolute ([Fig. 1a](#)), nor relative tree growth ([Fig. 1b](#)). Similarly, we found no significant relationships at the individual level, which however, in contrast to our expectation, showed a marginally significant negative slope ([Fig. 1c](#)). Removing the coniferous trees from the analysis ([Fig. 1d](#)) did not affect this relationship.

Coordination of leaf traits

The PCA of the leaf traits is shown in [Fig. 2a](#). The trait space of the conifers pine *P. sylvestris* and spruce *P. abies* overlapped, but was mostly separated from broadleaved trees. The trait space of ash *F. excelsior* only partially overlapped with linden *T. cordata*, while there was hardly no overlap with oak *Q. petraea* and beech *F. sylvatica*. The strongest overlap showed oak and beech, partly overlapping with linden as well. Separate analyses for broadleaved trees ([Fig. 2b](#)) and conifers ([Fig. 2c](#)) revealed vastly different relationships between the leaf traits for these groups (see the Supporting information

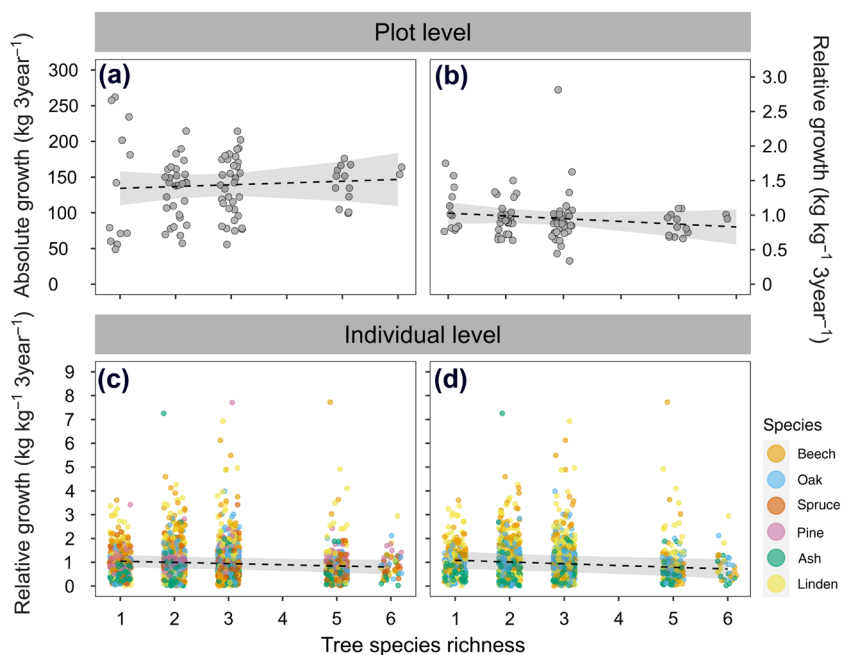


Figure 1. Growth as a function of tree species richness, at the plot level (a–b) and at the level of individual trees (c–d). All plots share the same x-axis that indicates tree species richness. Grey dots indicate individual plots (a–b), coloured dots indicate individual trees (c–d). Dashed lines are based on the predictions of the underlying models (Table 1 for the results of the models), and the grey ribbon indicates the 95% confidence interval of these models. (a) Absolute increase in plot level woody biomass ($p=0.955$). (b) Relative increase in plot level woody biomass ($p=0.445$). (c) Relative growth at the individual level ($p=0.099$). (d) Relative growth at the individual level excluding spruce and pine ($p=0.055$).

Table 1. Anova results on the different hypotheses. (A) Results of four separate models explaining tree growth as a function of tree species richness. (B) Results of two separate models explaining mean trait scores and leaf trait variation as functions of tree species richness and light extinction coefficient. (C) Results of a model explaining tree growth as a function of mean trait scores, leaf trait variation, tree species richness and light extinction coefficient jointly. All sums of squares (Sum. sq.), mean squares (Mean sq.), numerator degrees of freedom (numDF), denominator degrees of freedom (denDF), F-values and p-values refer to type III Anova results. Significant results ($p < 0.05$) are highlighted in bold font.

Response	Predictor	Sum sq.	Mean sq.	numDF	denDF	F-value	p-value
(A)							
Absolute increase in plot level woody biomass	Tree species richness	1.0×10^{10}	1.0×10^{10}	1	45.39	0.003	0.955
Relative increase in plot level woody biomass	Tree species richness	0.024	0.024	1	39.77	0.592	0.445
Relative growth at individual level	Tree species richness	2.206	2.206	1	87.49	2.769	0.099
Relative growth at individual level (excl. conifers)	Tree species richness	4.057	4.057	1	84.63	3.780	0.055
(B)							
Mean trait scores	Tree species richness	16.898	16.898	1	55.47	16.483	< 0.001
	Light extinction coefficient	2.513	2.513	1	131.69	2.451	0.119
Leaf trait variation	Tree species richness	8.094	8.094	1	46.24	25.284	< 0.001
	Light extinction coefficient	2.654	2.654	1	141.66	8.290	0.004
(C)							
Relative growth at individual level	Leaf trait value	0.129	0.129	1	132.88	1.100	0.296
	Leaf trait variation	0.712	0.712	1	124.38	6.069	0.015
	Tree species richness	0.166	0.166	1	61.84	1.416	0.238
	Light extinction coefficient	0.147	0.147	1	95.20	1.253	0.265

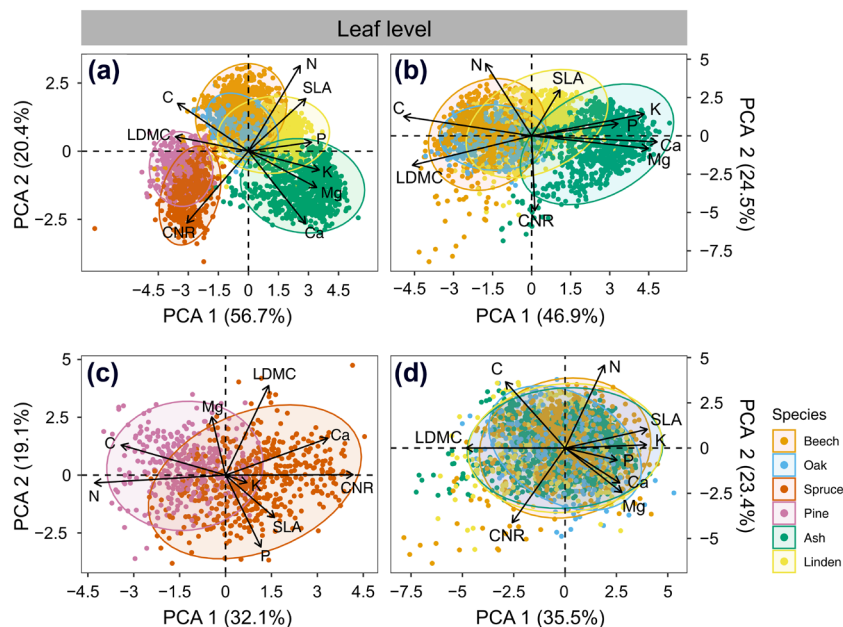


Figure 2. Principal component analysis (PCA). First versus second axes. Dots indicate individual leaves, coloured by species. Circles include 95% of the data points of each species. (a) Unscaled version including all species. (b) Unscaled version including only broadleaved species. (c) Unscaled version including only conifers. (d) Scaled version including only broadleaved species. Leaf traits were centred on the species mean trait values before conducting the PCA. LDMC, leaf dry matter content; SLA, specific leaf area; CNR, carbon-to-nitrogen ratio.

for single species analyses). For the broadleaved trees (Fig. 2b) all cations, SLA and leaf P showed positive loadings with the first PCA axis, whereas LDMC, leaf N and leaf C had negative loadings. Leaf N and SLA were positively and CN ratio was negatively aligned with the second PCA axis. In contrast, for the conifers (Fig. 2c), leaf N, leaf C and leaf Mg showed negative loadings with the first PCA axis, whereas LDMC, SLA, CN ratio, leaf P, leaf Ca and leaf K had positive loadings. Regarding the second PCA axis, LDMC, leaf C, leaf Mg and leaf Ca were positively aligned while SLA, leaf P and leaf K were negatively aligned.

When leaf traits of the broadleaved trees were centred on the species mean trait values (Fig. 2d), the amount of variation explained by axis 2 remained almost unchanged, while that of axis 1 decreased from 46.9 to 35.5%, i.e. by approximately one-quarter, which is the amount of variation only caused by species identity. The leaf traits still showed correlations with the first PCA axis which were similar to the previous PCA. The cations, SLA, leaf P and leaf N showed positive loadings, and LDMC, leaf C and CN ratio showed negative loadings on the first PCA axis. The almost congruent ellipses indicated a comparable amount of variation within species, with the notable exception of oak (blue ellipse) with a slightly lower variation compared to that of the other species.

Light, diversity and traits

We found that, with increasing tree species richness, mean leaf trait scores of the first axis of the centred PCA (Fig. 2b) increased. This indicated higher values on the LES, and thus more acquisitive leaves (Fig. 3a); whereas the SD decreased, which indicated lower trait variation along this axis, and thus less trait adjustments of leaves (Fig. 3b). The light extinction

coefficient had no significant effect on the mean scores (Fig. 3c) but a positive influence on leaf trait variation (Fig. 3d).

Influence of mean trait scores, leaf trait variation, light extinction coefficient and tree species richness on tree growth (Figure 4 shows the model predictions of relative growth of the individual trees as responses to mean trait scores (Fig. 4a), leaf trait variation (Fig. 4b), tree species richness (Fig. 4c) and light extinction coefficient (Fig. 4d). Combining these four predictors in a single model revealed that an increase in tree growth was primarily driven by leaf trait variation along the LES.

Mediators and covariate for the BPR

The results of the SEM (Fig. 5) confirmed the key role of leaf trait variation as mediator in the BRP. Whereas leaf trait variation decreased with tree species richness, relative tree growth increased with leaf trait variation, which resulted in a zero net effect of tree species richness on tree growth. This relationship was further modified by the mean leaf trait scores of the first PCA axis, which increased with tree species richness (i.e. leaf traits shifted to more acquisitive values), and which themselves reduced leaf trait variation (i.e. trees with a more acquisitive trait scores showed less trait variation). As mean leaf trait scores had no significant direct effect on relative growth, the BPR remained unaffected by this indirect pathway. Finally, the light extinction coefficient did not depend on tree species richness, but a greater light extinction coefficient increased leaf trait variation, which also indirectly contributed to enhanced tree growth. Applying the same SEMs to the single species resulted in a loss of most of the observed significant relationships (Supporting information), which was probably a result of the much lower statistical power with

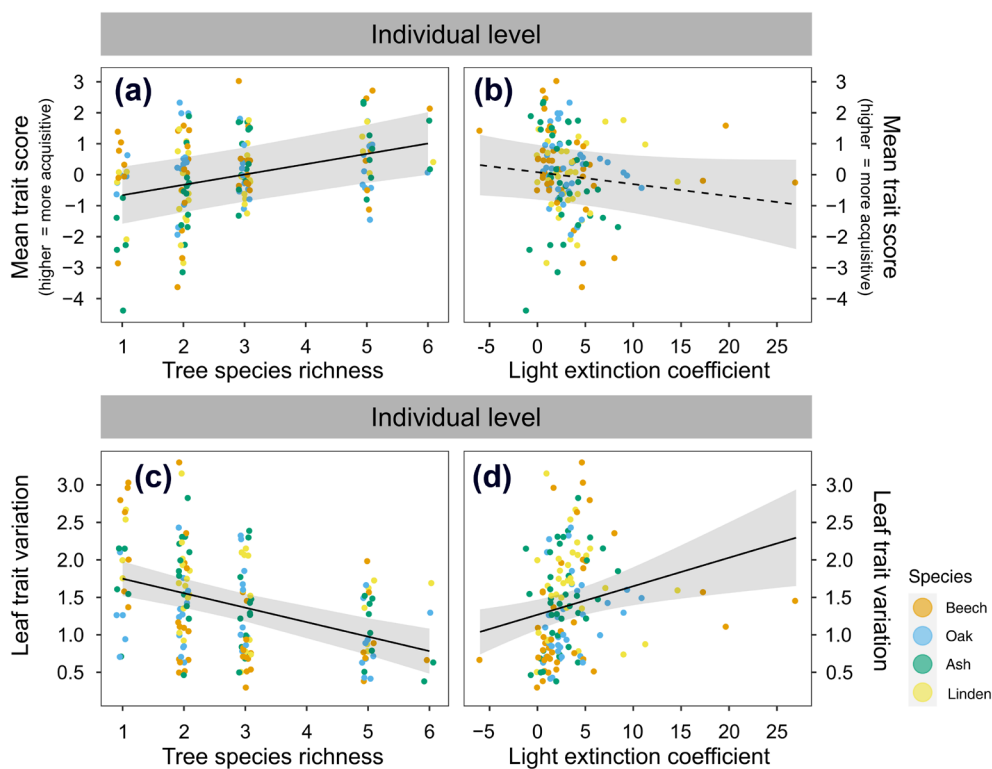


Figure 3. Effects of tree species richness and light extinction coefficient on mean trait scores of the first principal component analysis (PCA) axis and leaf trait variation expressed as the SD of these scores. Lines are based on the predictions of the underlying model, solid lines indicate significant effects and the dashed line indicates a non-significant effect (Table 1 for the results of the models). The grey ribbons indicate the 95% confidence interval of these models. Dots indicate individual trees, coloured by species. (a) Mean trait score versus tree species richness ($p < 0.001$). (b) Mean trait score versus light extinction coefficient ($p = 0.199$). (c) Leaf trait variation versus tree species richness ($p < 0.001$). (d) Leaf trait variation versus light extinction coefficient ($p = 0.004$).

using much fewer observations. An exception was the negative impact of mean leaf trait scores on leaf trait variation, which was consistent across all single-species models.

Discussion

Our study investigated the influence of tree species richness on tree growth in a biodiversity–ecosystem functioning experiment over a period of three years. Most strikingly, we were able to identify a connection between these two factors – albeit only for broadleaved trees and not for conifers. While we did not encounter a direct link between tree richness and productivity, we were able to identify leaf trait variation as the key mediating factor. An increase in biodiversity led to a decrease in leaf trait variation – but an increase in tree growth was caused by an increase in leaf trait variation (Fig. 5). Thus, the negative effect of tree richness on leaf trait variation cancelled out the positive effect of leaf trait variation on growth, which in summary resulted in the absence of a significant BPR.

Relationship between tree species richness and tree productivity

The experiment failed to confirm our hypothesis of a positive BPR in the particular study period, but nonetheless provided important insights on the mediators of this relationship.

We did not encounter a significant BPR at the plot level nor at the level of individual trees; neither with including or excluding dead trees; nor when based on the full set of all six species; nor when conifers were excluded.

While a positive BPR has been largely confirmed for natural forest ecosystems (Liang et al. 2016), several studies in planted forest diversity experiments reported a non-significant BPR, as summarized by Kambach et al. (2019). A non-significant BPR might be brought about, for example, by strong differences in species-specific growth performances (Nguyen et al. 2012). Additionally, Tobner et al. (2016) argued that a high initial nutrient availability might reduce a potential biodiversity effect on growth. Finally, Guo and Ren (2014) also argued that a potential BPR might not be visible in the early stage of forest development. These mechanisms might also influence the Kreinitz experiment.

Regarding the differences in species performance, a potential factor in the Kreinitz experiment could be that here all ash trees showed signs of infection with *Hymenoscyphus fraxineus*, which is a fungus responsible for the large-scale ash dieback in central Europe. However, despite showing the lowest growth rate among all tree species, removing *F. excelsior* from the analysis had no effect on tree growth (Supporting information).

Similarly, a high soil nutrient availability could potentially play a role for the Kreinitz experiment, as it was established on former agricultural land which had obviously received

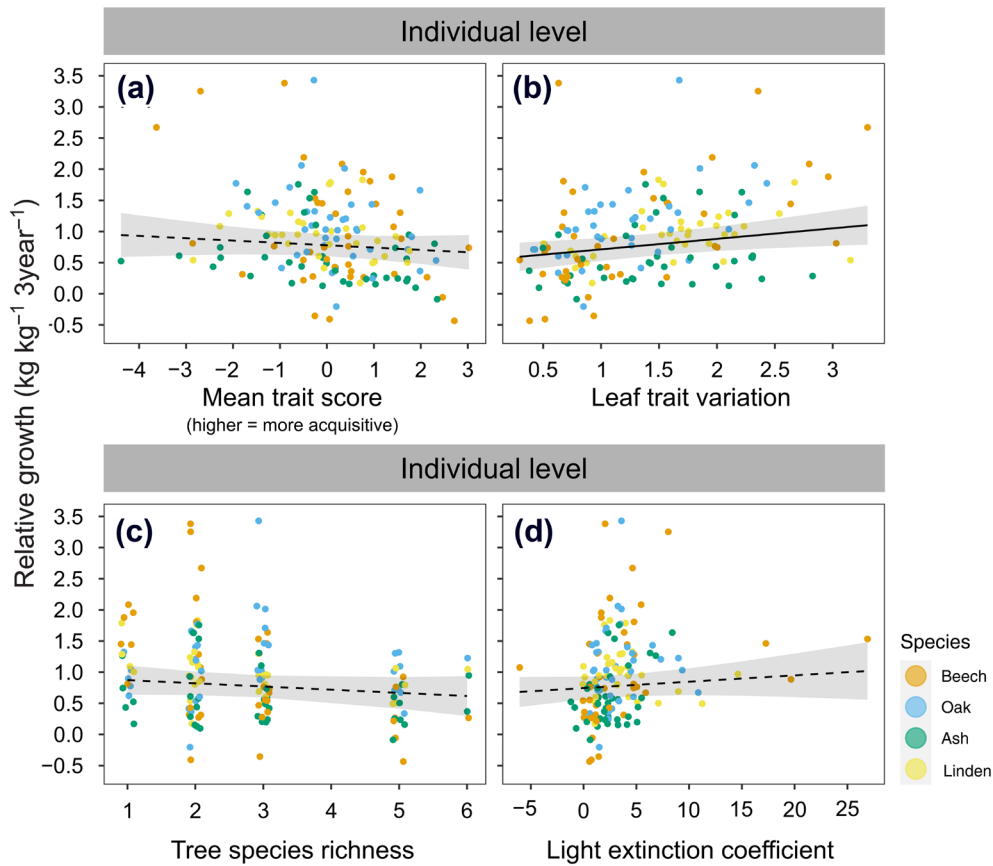


Figure 4. Relative growth as a function of mean trait scores (a), leaf trait variation (b), tree species richness (c) and light extinction coefficient (d). All plots share the same y-axis (relative growth of individual trees over three years). Lines are based on the predictions of the underlying model including all predictors (see Table 1 for the results of the models). The solid line indicates a significant effect (4b, $p=0.015$) and the dashed lines indicate non-significant effects (4a, $p=0.296$; 4c, $p=0.238$ 4d, $p=0.265$). The grey ribbons indicate the 95% confidence interval of the predictions. Dots indicate individual trees, coloured by species.

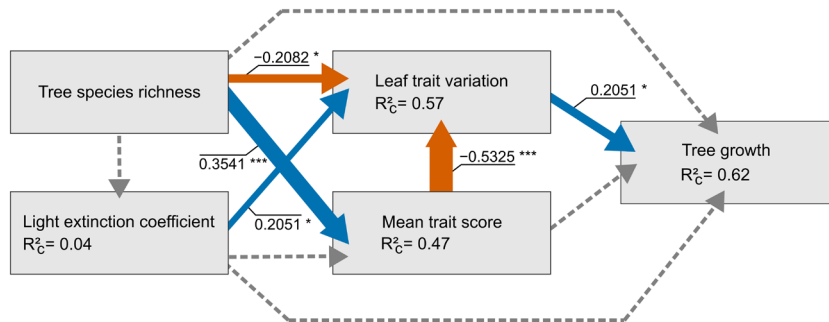


Figure 5. Path diagram derived from a structural equation model (SEM) describing the influence of plot tree species richness, light extinction coefficient, mean trait scores on the first PCA axis and leaf trait variation (SD of the scores) on tree growth. Boxes represent measured variables, arrows represent directional relationships among variables. Solid arrows indicate significant relationships, dashed arrows indicate nonsignificant relationships (** * $=p < 0.001$, $^* = p < 0.05$). Blue arrows indicate positive relationships, orange arrows indicate negative relationships. Width of the arrows is scaled according to the standardized regression coefficient, also indicated by the adjacent numbers. R^2_c indicates the conditional coefficient of determination based on both the fixed and the random effects of the models. When removing all non-significant relationship, global goodness-of-fit was fulfilled ($C = 11.961$; 8 df; $p = 0.153$).

large amounts of organic fertilizer (Landgraf 2001). A potential positive biodiversity effect on tree growth should be at least partially based on complementary usage of belowground resources (Houle et al. 2014, Teste et al. 2014). However, if soil nutrients are most likely not a limiting factor for tree growth, as might be the case for the Kreinitz experiment, nutrient-use niche partitioning as potential driver for a positive BPR could not come into play.

Finally, the Kreinitz experiment might have been in a too early stage of development to find a positive BPR. It was established in 2005 and the trees were at the time of the first and second measuring, at 8 and 11 years old. As BPR increase with time (Huang et al. 2018), it might be too early to detect significant effects. In addition, Guo and Ren (2014) pointed out that tree species differ in their speed of development, thus masking a potential BPR at this stage of the experiment.

However, the fact that we did not find a direct link between biodiversity and productivity does not mean that diversity effects did not play a role. There were several important mediators for the BPR that were driven by tree richness.

Influence of the light extinction coefficient and tree species richness on leaf traits

Coordination of leaf traits at the within-individual level

The results of the PCA demonstrate a considerable amount of intraspecific trait variation (ITV), as proposed for example by Albert et al. (2012) and Siefert et al. (2015). In our case, all species show a comparable amount of ITV (Fig. 2), which is consistent with other studies in forest ecosystems (Fyllas et al. 2020, Schmitt et al. 2020). This also includes *F. excelsior* (Fig. 2d), despite its infection with *H. fraxineus*. As the infection does not appear to affect the ITV, we would assume that it also did not affect the role of ITV as mediator. In our case, the trait alignment with the first PCA axis also reflects the conservative/acquisitive nature of the leaf traits in broadleaved trees. The acquisitive traits SLA, leaf P and the cations aligned closely with the first PCA axis, which is consistent with previous studies showing similar relationships at the species level (Lin et al. 2020, Jiang et al. 2021). Furthermore, the conservative traits LDMC and leaf C were negatively aligned with the first PCA axis, which is also in agreement with previous studies (Lin et al. 2020, Jiang et al. 2021).

Influence of tree species richness on leaf traits

We observed that with increasing tree species richness, leaf trait variation decreased and leaf traits shifted to more acquisitive values, which provides strong support for the first part of our second hypothesis (H2a).

The decrease of leaf trait variation with increasing tree species richness is in agreement with Proß et al. (2021) who reported a similar relationship. Thus, mixing different species allows leaves to stay more closely at the tree's mean values. In contrast, leaves of trees growing in monocultures show higher variation further away from the mean to increase light capture.

Furthermore, our results also confirm those of Davrinche and Haider (2021), who found a shift towards more

acquisitive leaf traits in more diverse forest communities. A possible explanation for this observation is that more diverse communities have a vastly different light regime compared to that of monocultures (Sapjanskas et al. 2014), and leaf traits might shift to more acquisitive values in response to inner canopy light conditions (Iio et al. 2005). However, a tree species richness effect on leaf traits can also occur independently of the diversity–light interaction (Benomar et al. 2011), for example as a response to differences in belowground resource use (Richards et al. 2010).

Influence of light on leaf traits

We could only partly confirm our second hypothesis that a higher light extinction coefficient results in shifts in mean trait scores and a higher leaf trait variation (H2b). While we encountered support for the latter (Fig. 5), we have to reject the former part of the hypothesis. Our finding that a higher light extinction coefficient results in a stronger leaf trait variation is also supported by reports in the literature (Niinemets et al. 2015).

The different responses of mean trait scores and leaf trait variation are consistent with results from Herrera et al. (2015) who demonstrated that, for the herb *Helleborus foetidus*, within-individual leaf trait variation was largely independent of plant mean trait scores.

Our findings suggest that individual trees broaden their trait space by diversifying their leaf traits, rather than shifting it to more acquisitive trait scores as a response to changes in light availability.

In the densely planted Kreinitz experiment, crown space could be the most limiting factor for tree growth. The strong competition for light might facilitate the optimisation of crown space for all individuals (Pretzsch 2014). For an individual tree, a densely packed, narrow crown would result in a steep light interception curve and consequently a steep gradient in leaf traits. A tree with flexible leaf traits would have the benefit of a larger potential crown length that can be used for light capture. Across the whole tree, a directional shift of the leaf trait might not occur if the light conditions for the average leaf remained the same, but leaves expanded a steeper light gradient in both directions, either becoming more acquisitive at one end and/or more conservative at the other end of the light gradient.

Influence of mean trait scores, leaf trait variation, tree species richness and light extinction coefficient on tree growth

When we analysed the effects of the leaf's position on the LES axis, leaf trait variation, tree species richness and the light extinction coefficient on tree growth, we found that leaf trait variation was the only significant driver of tree growth (Fig. 5). The causal explanation for this finding would be that an increased variability of LES traits allows the tree to more effectively exploit the light gradient. We are not aware of any other study that was able to demonstrate this direct link between increased leaf trait variation and tree growth.

However, it is equally remarkable that a shift of the mean trait scores towards higher acquisitiveness did not have a similar effect on tree growth, as such a relationship was demonstrated before (Poorter and Bongers 2006, Chaturvedi et al. 2011, Li et al. 2017). A possible explanation could be that a shift towards higher acquisitiveness comes at the cost of lower leaf longevity at the within-individual level and higher susceptibility to herbivore and pathogen attack. However, evidence for this assumption is lacking so far. Anderegg et al. (2018) reported that leaf longevity and SLA are positively correlated within species, but it is unclear to which degree this is brought about by genetic differentiation within species or by phenotypic plasticity. In particular, the relationship between leaf longevity and SLA within individuals is unknown. If such tradeoffs exist, they might offset any positive effects of leaf trait shifts on growth.

Leaf trait variation is a mediator and light is a covariate for the BPR

We observed that the leaf trait variation mediates the influence of tree species richness on tree growth. In addition, the light extinction coefficient modified this interaction by increasing the leaf trait variation. In contrast, the leaf position on the LES axis did not influence tree growth, which is why we can only partially confirm our fourth hypothesis.

We interpret these observations as a mechanism to adjust to changes in the available trait space, based on the limiting similarity theory (MacArthur and Levins 1967). In monocultures, the similarity between individuals could be a limiting factor for tree growth, as individuals of the same species occupy the same trait space (Violle et al. 2012). However, it seems that trees partially compensate for this negative effect of limiting similarity on growth by diversifying their leaf traits.

In plots with higher tree species richness, the different species might be already sufficiently diverse regarding their leaf traits to show optimal growth. This would be compatible with observations by Benavides et al. (2019), who observed a reduction in species level trait space as a reaction to increased tree species richness. However, in order to reach the upper canopy faster, trees might shift their traits towards more acquisitive values (Pellis 2004). In this scenario, the majority of the trees might actually grow close to their optimal growth rate, which would explain the absence of a clear diversity effect on growth.

In conclusion, the absence of a positive BPR in forests does not mean that there is no relationship between tree richness and tree growth. It seems that tree richness operates both through increased acquisitive trait scores and leaf trait variation, two processes that can cancel out each other and result in the absence of a significant effect of tree richness on productivity. These two opposing mechanisms might be the reason for the absence of positive BPRs in the literature. However, unless we have more data on the within-tree trait variation, we can only speculate whether these findings only apply to the unique situation of the Kreinitz experiment in Germany or whether they offer a general explanation for the negative

(Firn et al. 2007) or non-significant BPR (Nguyen et al. 2012, Staples et al. 2019) described in the literature. A plausible mechanism would be that the direction of the BPR depends on which factor is more strongly influenced by the tree species richness. A scenario where the tree species richness effect dominates the leaf trait variation could result in a negative BPR. Conversely, if the species richness effect on leaf traits predominates, a positive BPR would be more likely. Which of these factors is more strongly influenced by tree species richness might be dependent on several other factors. In any case, our results point to the importance of within-individual leaf trait variation as one important moderator in BPRs.

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Author contributions

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Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.8387670> (Proß et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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