



# Disentangling tree species identity and richness effects on the herb layer: first results from a German tree diversity experiment

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## Keywords

Biomass; BIOTREE; Compositional turnover; Functional biodiversity research; FunDivEUROPE; Herb layer species richness; Nutrient cycling; Vegetation ecology

## Nomenclature

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## Abstract

**Questions:** The forest herb layer provides a multitude of ecosystem services as a result of its species-rich character. Herb layer diversity and biomass are both influenced by tree layer composition and species richness through species-specific influences on environmental conditions. The results of observational studies on richness–biomass relationships between tree and herb layer have not been unequivocal. We examined tree species identity and richness effects on herb layer species richness, composition, biomass and nutrient concentrations in young experimental tree plantations.

**Location:** BIOTREE tree diversity experiment, Kaltenborn, Germany.

**Methods:** Sixteen plots were planted in 2004, using a pool of four tree species (beech, oak, Douglas-fir, Norway spruce) and four richness levels, comprised of all possible species combinations. In this way, complete dilution was avoided, allowing separation of tree species identity and richness effects. Mixed plots consisted of a matrix of monospecific patches. One permanent vegetation quadrat of 1 m<sup>2</sup> was established in the centre of four patches per plot. The herb layer was monitored in 2004 and 2010; in 2010 light measurements were performed in each quadrat, and in 2011 above-ground biomass was sampled on 0.25 m<sup>2</sup> within the quadrat.

**Results:** Community composition shifted markedly between 2004 and 2010. Tree species identity did not yet influence temporal compositional turnover or herb layer species richness in 2004 and 2010. Ellenberg N indicated a temporal shift towards lower soil fertility under all tree species, whereas Ellenberg R indicated decreasing soil acidity under beech and Douglas-fir. Ellenberg L and F showed no shift from 2004 to 2010. Apart from the significantly lower Ellenberg N for beech, none of the Ellenberg indicators indicated interspecific differences. Douglas-fir, and especially Norway spruce, negatively influenced total above-ground herb layer biomass. Douglas-fir also induced lower relative light availability, higher potassium, magnesium and nitrogen concentrations and lower carbon:nitrogen ratios in the total biomass. Higher tree species richness positively affected graminoid and total biomass and also slightly increased plot-level herb layer species richness.

**Conclusions:** Despite the young age of the experiment, tree species identity and richness effects on the herb layer could be discerned. We expect these relations to become stronger with time.

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## Introduction

The herb layer accounts for most of the total plant diversity in temperate forest ecosystems, and, as a result of its high diversity, it provides a multitude of non-timber forest products and many habitats for mammals and insects (e.g. Fayt et al. 2006; Marshall & Hawthorne 2012). It contributes to the annual litter production and nutrient cycling (Muller 2003), and through the resource competition with germinating seedlings, the herb layer community also influences the future composition of the shrub and tree layer (Gilliam 2007). In general, a higher biodiversity increases the efficiency by which ecological communities capture resources, produce biomass, decompose and recycle nutrients, which leads to increasing ecosystem stability (Cardinale et al. 2012). Hector & Bagchi (2007) and Isbell et al. (2011) indicated that different species promote different functions in different years, at different locations and under different environmental conditions. This promotes the precautionary principle of conserving maximum biodiversity in order to obtain long-term forest ecosystem stability and provisioning of ecosystem services. In this respect, it is essential to know how tree layer diversity affects the herb layer.

Trees have a species-specific impact on local environmental conditions. Messier et al. (1998) found differences among tree species in the mean amount, variability and nature of the light reaching the forest floor. Tree species-specific effects on the amounts of throughfall, transpiration and water uptake by roots result in significant differences in soil water content among tree species (e.g. Barbier et al. 2008, 2009; Geißler et al. 2012). Soil nutrient availability and acidity are also known to be influenced by the composition of the tree layer, as a result of tree species-specific differences in litter quality and quantity, nitrogen fixation, nutrient uptake and atmospheric deposition on leaves and needles (e.g. Augusto et al. 2003; Hagen-Thorn et al. 2004). In addition, phytotoxic compounds in the litter of certain tree species and a thick litter layer may negatively affect germination and performance of herb layer species (Rodríguez-Calcerrada et al. 2011). As a consequence of these tree species identity effects, the composition of the tree layer may substantially affect herb layer composition and biomass, as species in the herb layer need specific environmental conditions for optimal growth (e.g. Ellenberg & Leuschner 2010). Van Calster et al. (2008) and Meers et al. (2010) noticed significant changes in herb layer composition after conversion of the tree layer composition, while Légaré et al. (2001) observed differences in herb layer cover.

The overall influence of tree species richness on the forest stand-level environmental conditions, and therefore

the herb layer diversity, biomass and nutrient stocks, can be decomposed into additive and non-additive effects. In a forest stand composed of multiple tree species, the local presence and abundance of individual tree species may lead to a patch-scale pattern of environmental conditions where each patch mirrors the sole influence of the present tree species without interacting with other surrounding tree species (Yankelevich et al. 2006; Morin et al. 2011). The effect of tree species richness on the environmental conditions is then additive, as it results from identity effects of the component tree species. The stand level environmental conditions are then more or less the weighted average of the individual tree species effects. According to the resource heterogeneity hypothesis (Ricklefs 1977; Huston 1979), environmental heterogeneity in a mixed forest stand leads to differences in herb layer composition between the patches ( $\beta$ -diversity), resulting in a higher herb layer species richness at the stand level ( $\gamma$ -diversity) compared to a monospecific forest stand. The herb layer species pool of the mixed forest stand will then be similar to the total species pool of the monocultures of the component tree species. Environmental heterogeneity may also lead to higher biomass in the herb layer, as herb layer species are more likely to find optimal growth conditions in variable environments (Vockenhuber et al. 2011). In contrast, tree species in close contact may also interact, leading to the creation of new environmental conditions throughout the forest stand, and hence non-additive tree species richness effects on the environmental conditions and the herb layer. For example, Ball et al. (2008) found that the mixing of litter in stands with multiple tree species may induce non-additive effects on litter N content, while the results of Dijkstra et al. (2009) indicated a non-additive effect on soil C respiration and net N mineralization. Decomposition rates in litter mixtures may also differ from the predictions based on single species (Wu et al. 2013), leading to differences in nutrient availability and soil acidity. These new environmental conditions create opportunities for species that were not yet present in the component monocultures. Other herb layer species may be lost compared to the component monocultures, if the new environmental conditions no longer match their niche requirements. The stand-level herb layer species richness and biomass of a mixed forest stand may then be higher, equal or even lower than in a monospecific forest stand. In reality, there is always a mix of additive and non-additive effects of tree species richness on the environmental conditions. A more intimate mixture of tree species will probably induce weaker additive effects and stronger non-additive effects as more interspecific interactions take place.

The results of studies on the impact of tree layer diversity on herb layer diversity (Barbier et al. 2008; Mölder et al. 2008) and biomass (Cavard et al. 2011; Vockenhuber et al. 2011) have not been consistent. Most of these results were derived from observational studies in mature forests, where it was not possible to distinguish between additive and non-additive effects, and which often do not have an orthogonal design, i.e. they are not able to detect and quantify an effect of tree species richness against a background of tree species identity effects and other confounding factors (e.g. soil characteristics; Nadrowski et al. 2010). To overcome this problem, Both et al. (2011) recommended using experimental approaches. The relatively young German BIOTREE biodiversity–ecosystem functioning experiment is designed in a way that allows disentangling tree species identity and richness effects in the absence of confounding factors. Moreover, in this early development stage, tree species interactions and hence novel environment creation (i.e. the non-additive effect of tree species richness) only occur at the borders between the small monoculture patches in BIOTREE’s mixed plots (see below) and are therefore negligible. This enables us to examine the effect of resource heterogeneity between the patches (i.e. the additive effect of tree species richness). BIOTREE concentrates on two pairs of ecologically similar species: two deciduous species *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl./*Quercus robur* L., and two evergreen coniferous species *Pseudotsuga menziesii* (Mirb.) Franco and *Picea abies* (L.) Karsten. All species prefer nutrient-poor to moderately nutrient-rich soils. *Quercus* sp. and *P. menziesii* display an intermediate degree of shade tolerance, while *F. sylvatica* and *P. abies* are characterized by a high shade tolerance (Tree Database, Forest Ecology and Forest Management Group, Wageningen University, NL). Herb layer surveys were conducted directly after the experiment was established (2004) and 6 yr later (2010/2011). We hypothesized that:

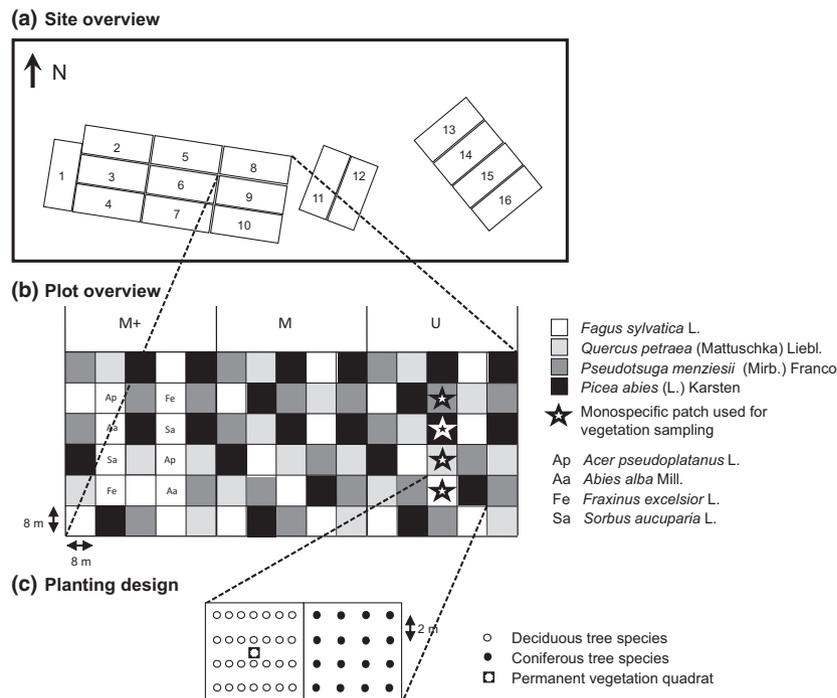
- 1 The composition of the herb layer shows a clear temporal turnover due to tree canopy development. The acidifying effect, fast growth and evergreen nature of the coniferous species leads to a lower share of light-demanding herb layer species that are sensitive to soil acidification in herb layers influenced by these tree species (‘identity effect’);
- 2 The species-specific impact of the examined tree species on environmental conditions induces differences in herb layer species richness, biomass, nutrient concentrations and C:N and N:P ratios in the herb layer biomass (‘identity effect’ on the patch level);
- 3 Resource heterogeneity induced by tree layers with higher species richness positively influences herb layer species richness and biomass (‘richness effect’ on the forest stand level).

## Methods

### Site information and experimental set-up

As part of a worldwide network of tree diversity experiments, the German BIOTREE biodiversity–ecosystem functioning experiment aims at quantifying the relations between tree layer species richness/composition and forest ecosystem characteristics, processes, functions and services. It consists of three sites ([www.treedivnet.ugent.be](http://www.treedivnet.ugent.be); Scherer-Lorenzen et al. 2007). Our study was performed at the ‘Kaltenborn’ site in the proximity of Kaltenborn (10°13′ E, 50°47′ N), situated at 325 m a.s.l. in the Southern Thuringian Trias, a region with a sub-Atlantic climate. The mean annual precipitation was 765 mm and the mean annual temperature 8.5 °C during the period 1981–2010 (German Meteorological Service, [www.dwd.de](http://www.dwd.de); weather station Eisenach). The soil is an Orthoeutric Arenosol (FAO 2005) with sandstone bedrock beneath a 100-cm deep loamy sand mineral layer. The 23-ha site neighbours a forest dominated by pine and beech on the southern side, and grassland on the northern, eastern and western sides. The natural vegetation of the site is beech-dominated deciduous forest. It was formerly used as cropland and in 1975 converted to grassland with a yearly mowing cycle and some grazing.

Sixteen plots of 120 m × 48 m were established and planted with 3- and 4-yr-old seedlings in 2003–2004 (Fig. 1). The species pool used consists of deciduous species *Fagus sylvatica* L. (beech) and *Quercus petraea* (Mattuschka) Liebl./*Quercus robur* L. (oak), and coniferous species *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) and *Picea abies* (L.) Karsten (Norway spruce). These species were chosen based on the local growing conditions and the afforestation recommendations of the forest administration, and are important species for regional forestry. This maximizes the representativeness of the experiment to real-world forests (Nadrowski et al. 2010). The trees were planted in different combinations and at different levels of tree species richness. All possible species permutations were used to create the richness gradient: four monocultures, six-two-species mixtures, four-three-species mixtures and two replicates of the four-species mixture. A complete dilution design (i.e. a design with monoculture stands of only one species, combined with a species richness gradient including this monoculture species in all mixtures) (Baeten et al. 2013) was thus avoided, and the design allowed us to unambiguously separate tree species richness effects from tree species identity effects (Nadrowski et al. 2010). Moreover, within every tree species richness level, the component tree species were planted in equal amounts. Maximizing evenness is an appropriate way to study tree species richness effects with-



**Fig. 1.** Experimental setup and planting design. **(a)** The sixteen plots of 120 m × 48 m; **(b)** Detailed view of a four-species plot: each plot is divided into three equal subplots of 40 m × 48 m: an unmanaged subplot (U), a subplot managed according to close-to-nature forestry (M) and a subplot managed according to close-to-nature forestry in which additional species were planted (M+). Every subplot is composed of small monospecific patches of 8 m × 8 m, and vegetation sampling was performed in the middle patch of the second till the fifth row of the unmanaged subplot; **(c)** Planting design and location of the vegetation quadrat: the monospecific patches contain seven by four trees for deciduous species (*F. sylvatica*, *Q. petraea*) and four by four trees for coniferous species (*P. menziesii*, *P. abies*). The permanent vegetation quadrat is located at the centre of the monospecific patch (modified from Scherer-Lorenzen et al. 2007).

out the potential confounding effect of differences in tree species abundance, although Schmitz et al. (2013) found consistent effects of biodiversity on ecosystem functioning even under varying density and evenness. Tree species richness levels and tree species combinations were randomly allocated to the plots. Each plot was divided into three equal subplots of 48 m × 40 m, and each subplot consisted of six rows of five monospecific patches of 8 m × 8 m. Slow- and fast-growing tree species were planted simultaneously, and the patch planting design allowed us to avoid dominance of fast-growing tree species and out-competition of slower-growing ones. Within the monospecific patches, self-thinning processes (or silvicultural thinnings in the 'managed' subplot) will result in the survival of few or even single individuals per patch, leading to an intimate mixture of all species planted at a later stage. In this way, the tree species mixture can be maintained in the longer term and the experiment will look more like a natural tree-by-tree mix. This planting in groups is a possible practice in silviculture if the aim is to ensure intimate mixtures in the long term. Coniferous patches were planted as four by four trees, while deciduous

patches held four rows of seven trees each (reflecting tree densities common in silvicultural practice). Increasing the density of the deciduous species has been done to balance the fast growth of coniferous vs deciduous trees. Hence, slow-growing deciduous trees were planted in higher density to achieve more similar canopy cover. This is a common practice in plantations, which makes our design representative. Hence, the tree species identity effect has been given a wide interpretation at BIOTREE, containing effects on e.g. litter quality, light availability but also an effect of tree density. The planting design, or the allocation of the tree species to the patches, was equal for all three subplots per plot. Up to 2011, the three subplots had not been treated differently and were kept without any management, apart from replanting dead individuals, removal of spontaneously established trees and mowing in order to ensure successful establishment until 2008. Two of the three subplots will be managed according to close-to-nature forestry schemes (these subplots were not examined in this study) and one of these two subplots was planted with four additional tree species, each planted in two patches (for a detailed description of

the experimental design, see Scherer-Lorenzen et al. 2007). In 2010, mean tree height was 2.07, 2.41, 3.25 and 3.45 m for beech, oak, Norway spruce and Douglas-fir, respectively. Crown closure was not yet reached although tree crowns sometimes overlapped in the basal crown part, especially for Norway spruce and Douglas-fir.

### Data collection

In June 2004 and 2010, vegetation surveys were performed in four permanent vegetation quadrats of 1 m × 1 m in the unmanaged subplot of each plot ( $n = 64$ ). The vegetation quadrats were located in four central patches of the subplot (Fig. 1) and positioned in the centre of the monospecific patches. Every quadrat was thus completely surrounded by one single tree species (factor 'tree species'). In this way, in the full-grown phase of the experiment, it will be possible to: (1) compare the influence of a specific tree species between different tree species diversity levels; e.g. *Fagus sylvatica* may have a different effect in a monoculture (pure tree species identity effect) compared to a three-species mixture (due to a combination of tree species identity and diversity effects); and (2) compare the influence of different tree species within one plot to see whether a patch-scale pattern of individual tree species effects is created, or whether new environmental conditions are created due to interactions between the different tree species within one plot. All species in the herb layer (<1.3 m), including woody species, were identified and their percentage cover estimated. Species names follow the nomenclature of Jäger (2008). In June 2010, four PPFD (photosynthetic photon flux density) measurements were performed in every quadrat, using two LiCor quantum sensors (LI-190) and loggers (LI-1400, LiCor Corp., Lincoln, NE, US), which simultaneously measured light availability in the quadrat at 1-m height and above the trees (reference). The relative light availability was then calculated by taking the ratio between these two values. In June 2011, all herb layer above-ground biomass within a frame of 0.5 m × 0.5 m, placed at a representative location within each quadrat, was clipped. The total biomass sample was subdivided into the fractions 'graminoids' and 'herbs'. Samples were dried for 48 hr at 70 °C, their dry biomass quantified, and then samples were ground and analysed for potassium (K), calcium (Ca), magnesium (Mg) (destruction with HNO<sub>3</sub> and HClO<sub>4</sub>, analyses by atomic absorption spectrometry), phosphorus (P) (destruction with HNO<sub>3</sub> and HClO<sub>4</sub>, addition of H<sub>2</sub>SO<sub>4</sub>, ammonium paramolybdate and malachite green, analyses by spectrophotometry), of carbon (C) and nitrogen (N) (Elementar analyzer, type Vario Macro Cube in configuration CNS, with argon as carrier gas).

### Data analysis

All data analyses were performed in R 3.0.1 (R Foundation for Statistical Computing, Vienna, AT). In order to test for changes in vegetation composition following afforestation (first hypothesis), we calculated pair-wise dissimilarities on the full matrix containing quadrat-level herb layer community data (2004 and 2010), using Lennon (based on presence/absence data; Lennon et al. 2001) and Bray-Curtis (based on cover data) distance measures. The Lennon distance metric quantifies true compositional turnover and is not influenced by richness differences, such as derived from nestedness patterns (Baselga 2010). Non-metric multidimensional scaling (NMDS) was used to visualize the compositional differences. The significance of the compositional differences between the two survey years was tested with a permutational multivariate analysis of variance (PERMANOVA; *vegan* package; Anderson 2001). Permutations ( $N = 999$ ) were constrained within quadrats to account for the paired nature of the design. In addition, we examined the quadrat-level compositional differences in function of the tree species by separately analysing the data matrices of 2004 and 2010, using the Lennon and Bray-Curtis distance measures. In this way we tried to find out whether the vegetation composition already differed between quadrats surrounded by different tree species in 2004 (at the start of the experiment) and whether the surrounding tree species significantly influenced the vegetation composition towards 2010. Then we performed a separate indicator species analysis for the 2004 and 2010 survey data, with tree species as *a priori* classification variable (function *multipatt* in *indicspecies* package). Next, ANOVA was used to explore the sole effect of factor 'tree species' at quadrat level (1) herb layer species richness; (2) mean Ellenberg light (L), reaction (R), soil fertility (N) and moisture (F) values weighted by species cover for 2004 and 2010 separately; (3) compositional turnover (using Lennon distance) between the two surveys; and (4) relative light availability. Ellenberg values are widely used indicator values expressing species' preferences for some environmental variables on an ordinal scale (Ellenberg & Leuschner 2010). We use them as proxies for the environmental conditions induced by the tree species. Unfortunately, Ellenberg values were missing for 2–56% of the species (percentage dependent on the Ellenberg indicator and the year).

The second and third hypothesis required us to unravel tree species identity and richness effects on herb layer species richness, biomass of graminoids and herbs and total, nutrient concentrations and nutrient ratios, and this was done using a mixed model approach, based on quadrat-level data of 2010, i.e. an integrative method that takes

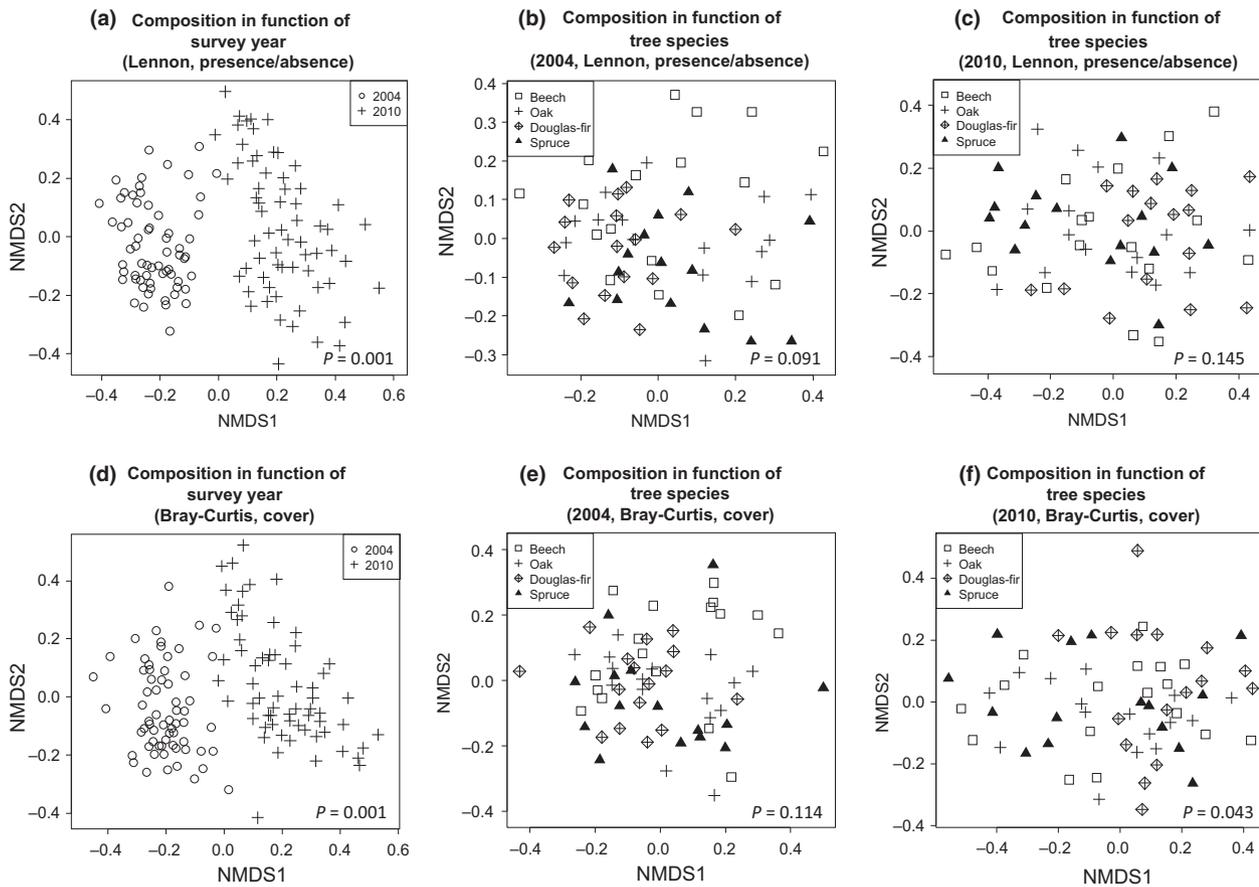
into account the effects of multiple potential fixed and random predictors. To start, effects for the plot level tree species richness (*TreeSR*; considered as a numeric value) and the quadrat-level tree species (*Tree species*; presence/absence data) were fitted, allowing for random variation across plots with potential plot level variation in the tree species effects [R-syntax:  $y \sim -1 + \text{TreeSR} + \text{Tree species} + (\text{Tree species} | \text{PlotID})$ ]; using *glmer* with a Poisson distribution family with a log model link function for herb layer species richness (not over-dispersed) and *lmer* with a Gaussian distribution family for the other response variables, both from the *lme4* package]. For a better interpretation of the coefficients, the model structure contained '-1' to remove the intercept from the model. For each response variable, we looked for model parsimony, first by sequentially reducing the random structure and keeping the fixed effect terms (approach according to Zuur et al. 2009): we subsequently dropped the plot-level variation in tree species effects [ $y \sim -1 + \text{TreeSR} + \text{Tree species} + (1 | \text{PlotID})$ ] and the random effect for plot identities [R-syntax:  $y \sim -1 + \text{TreeSR} + \text{Tree species}$ ; using *glm* from the R stats package) with a Poisson distribution family, log model link function and parameter estimation via maximum likelihood for herb layer species richness and *gls* from the *nlme* package, with a Gaussian distribution family and parameter estimation via restricted maximum likelihood for the other response variables]. The model with the lowest AIC (Akaike's information criterion; Akaike 1973) was regarded as most consistent with the data. However, models that differed <4 in AIC were considered equivalent (Burnham & Anderson 2004), and in this case, preference was given to the less complex model. Once an optimal random structure was found, we searched for the optimal fixed effect structure by comparing the AIC of models with the same random effect structure but a different fixed effects structure (here parameter values were maximum likelihood estimates; Zuur et al. 2009). We also fitted a model only containing an intercept. For each model, we calculated  $R^2$ , which refers to the fraction of the total variation in the response variable explained by the model. For models with fixed effects only, the adjusted  $R^2$  of the linear model was reported; for models that (also) contained random effects, a conditional  $R^2$  was calculated according to Nakagawa & Schielzeth (2013) (*MuMIn* package), indicating the proportion of the variance explained by both the random and fixed effects (not yet applicable for *glmer* with a Poisson distribution family).

The third hypothesis was further tested by quantifying plot-level herb layer species richness (based on species presence/absence in the four quadrats together) and total biomass (sum of quadrat level biomass values) and evaluating the trend in function of tree species richness using Pearson's product moment correlation coefficient.

## Results

We recorded a total of 50 herb layer species in 2004, and 60 in 2010 (App. S1). Indicator species analysis based on herb layer composition resulted in *Festuca rubra* as an indicator for Douglas-fir in 2004 and beech in 2010, and *Anthriscus sylvestris*, *Elytrigia repens*, *Urtica dioica*, *Vicia* sp. for Douglas-fir in 2010 and *Cirsium arvense*, *Tragopogon pratensis*, *Vicia sepium* as indicators for Norway spruce in 2010 (App. S2). Compositional dissimilarities based on Lennon and Bray-Curtis distance measures indicated that herb layer community composition shifted significantly between 2004 and 2010 (Fig. 2a,d). None of the surveys indicated a difference in herb layer composition between quadrats surrounded by different tree species, when based on presence/absence data (Fig. 2b,c). Compositional dissimilarities based on cover data also did not show a significant difference between tree species in 2004 ( $P = 0.114$ ; Fig. 2e), but this contrasted with the results of 2010 ( $P = 0.043$ ; Fig. 2f). The mean species richness of the herb layer in the vegetation quadrats was lower in 2010 than in 2004 for all tree species, without any significant difference between tree species (Fig. 3a). The compositional turnover was similar for the different tree species (Fig. 3b). The mean Ellenberg L values did not change between 2004 and 2010, and showed no significant differences between the tree species in 2004 nor in 2010 (Fig. 3c), although the relative light availability was lower for Douglas-fir compared to beech, oak and Norway spruce ( $P = 0.053$ ; App. S3). The mean Ellenberg R increased for beech and Douglas-fir and decreased for oak and Norway spruce from 2004 towards 2010 (Fig. 3d), but there was no difference between the tree species in 2004 and 2010. The mean Ellenberg N showed a clear decrease from 2004 towards 2010 for all tree species (Fig. 3e). In 2004, the mean Ellenberg N was significantly lower in the beech plots, indicating lower soil fertility compared to the other tree species. The mean Ellenberg F showed no changes from 2004 towards 2010 and did not differ significantly between tree species in 2004 and 2010 (Fig. 3f).

According to the model results based on data of 2010 (Table 1), none of the examined variables showed tree species identity effects differed between plots, as the random plot-level effect for tree species was never retained. Neither the tree species richness of the plot nor the identity of the tree species that surrounded the quadrat seemed to have affected quadrat-level herb layer species richness (in accordance with Fig. 3a), concentrations of Ca, P and C and the N:P ratio in the total biomass sample and herb layer biomass. Quadrat-level concentrations of K, Mg and N and the C:N ratio in the total biomass sample and graminoid and total biomass were significantly affected by the identity of the surrounding tree species. K, Mg and N

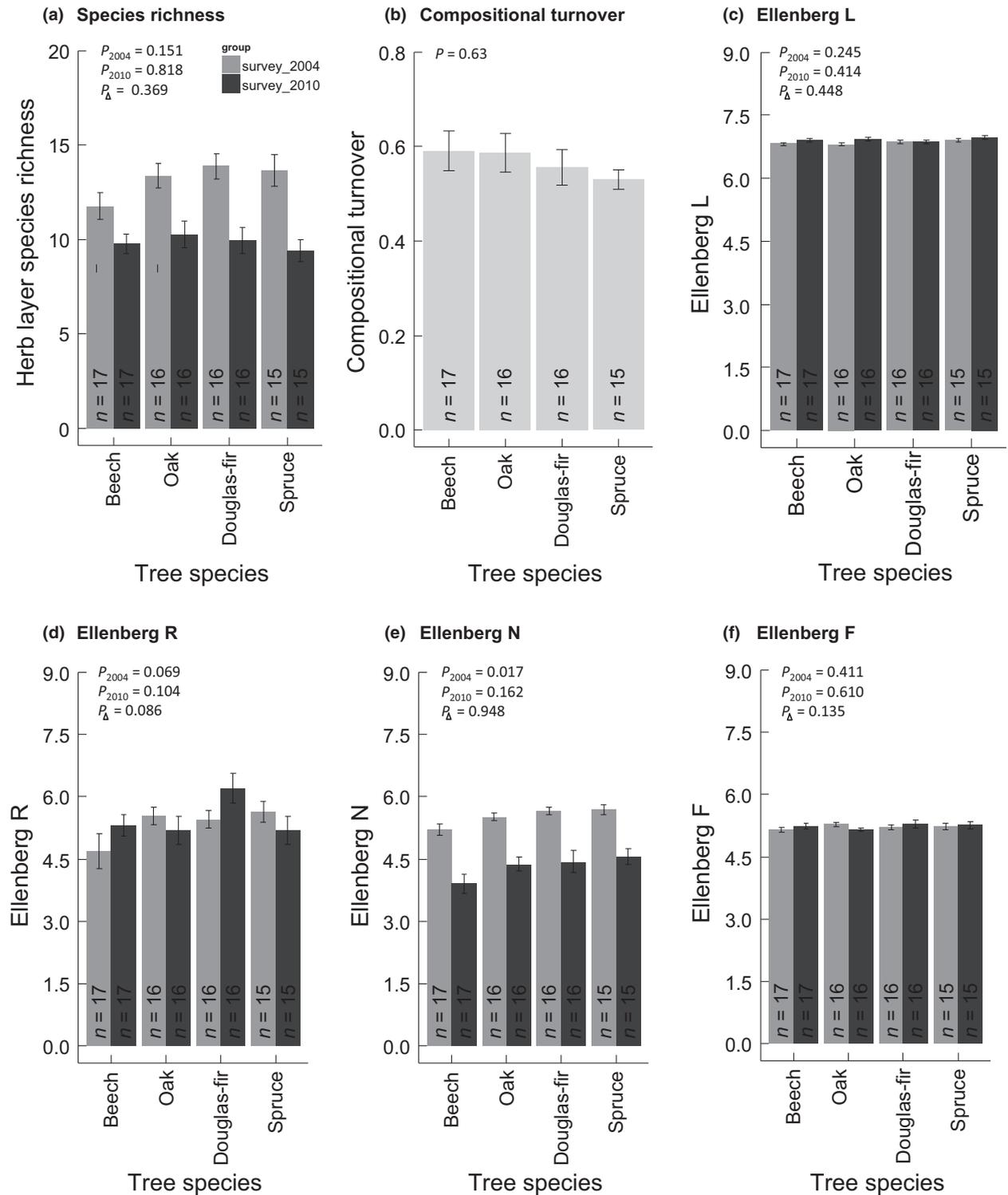


**Fig. 2.** Nonmetric Multidimensional Scaling based on composition (NMDS). NMDS of quadrats at the Kaltenborn site of the BIOTREE tree diversity experiment, **(a)** using Lennon distances based on herb layer presence/absence data in 2004 and 2010 in function of survey year, **(b)** using Lennon distances based on herb layer presence/absence data in 2004, and **(c)** 2010 in function of the surrounding tree species, **(d)** using Bray-Curtis distances based on herb layer cover data in 2004 and 2010 in function of survey year, **(e)** using Bray-Curtis distances based on herb layer cover data in 2004, and **(f)** 2010 in function of the surrounding tree species. The *P*-values are the outcome of the PERMANOVA, indicating the significance of the difference between the two survey years **(a, d)** or the tree species **(b, c, e, f)**.

concentrations in the total biomass sample were higher for Douglas-fir while C:N ratio was lowest for Douglas-fir compared to the other tree species. Quadrat-level graminoid and total biomass was lower for Douglas-fir and especially Norway spruce, compared to the deciduous species. Quadrat-level graminoid and total biomass showed a clear positive influence of the level of tree species richness. Quadrat-level results indicated that graminoid biomass was always higher than herb biomass (data not shown). Plot-level biomass of the herb layer significantly increased towards higher levels of tree species richness ( $P = 0.010$ ; Fig. 4a), in accordance with the quadrat-level model results. Plot-level herb layer species richness showed a slight increase from monocultures towards three-species mixtures, followed by a decrease for the four-species mixture, but differences were not significant ( $P = 0.806$ ; Fig. 4b).

## Discussion

The BIOTREE tree diversity experiment was installed in 2003–2004 on former grassland, characterized by typical environmental conditions, such as direct sunlight, no tree canopy rain interception, no extra litter input apart from the grass layer itself. During the first years after afforestation, the tree species influenced the environmental conditions and the herb layer in a similar way due to the small size and, hence, limited impact of the trees. In a later phase, the planted trees induced changes in environmental conditions compared to the grassland: interception of light and rain, changes in nutrient cycling and soil conditions (e.g. Messier et al. 1998; Barbier et al. 2009; De Schrijver et al. 2012). Since herb layer species differ in their environmental requirements, the environmental changes due to afforestation have affected the composition of the herb



**Fig. 3.** Temporal change in herb layer species richness, composition and Ellenberg values. **(a)** Herb layer species richness in 2004 and 2010, **(b)** compositional turnover (Lennon distance) between 2004 and 2010, **(c)** unweighted mean Ellenberg light-L, **(d)** reaction-R, **(e)** soil fertility-N and **(f)** moisture-F values in 2004 and 2010 in function of tree species for the quadrats at the Kaltenborn site of the BIOTREE tree diversity experiment (bars represent mean  $\pm$  SE;  $p_{2004}$  and  $p_{2010}$  indicate the significance of the difference in absolute values between tree species in 2004, respectively 2010,  $P_{\Delta}$  indicates the significance of the difference in shift from 2004 towards 2010 between tree species,  $P$  for compositional turnover indicates the significance of the difference between tree species (ANOVA results);  $n$  indicates the number of observations used for calculation).

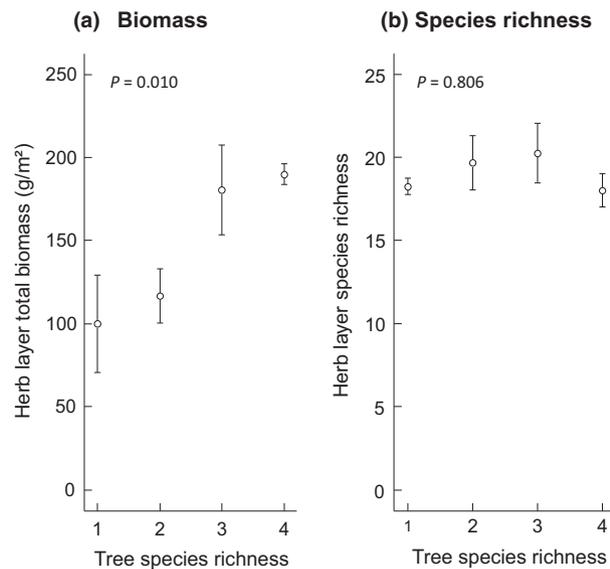
**Table 1.** Optimal mixed effects model structures for response variables. Results of mixed effects models relating the quadrat-level herb layer species richness, K, Ca, Mg, P, C and N concentrations and C:N and N:P ratios in the total biomass, and the graminoid ('Gram'), herb and total biomass ('biomass') of the survey in 2010 to the identity of the surrounding tree species and/or plot-level tree species richness. Models were selected based on AIC criteria – see main text for details on the structure of the full model and the step-wise reduction of the full model. Values are parameter estimates  $\pm$  SE. For models with a significant effect for tree species, the superscript letters indicate the results of a *post-hoc* test (Tukey's HSD): tree species followed by one or more equal letters do not differ significantly in their effect on the examined response variable. The random effect for plot identity was never significant.  $R^2$  refers to the fraction of variation explained by the optimal model structure ('-': not applicable for models containing only an intercept) ( $n$ : number of observations, values <64 are due to missing samples or samples too small for measurements).

Response Variable	$n$	$R^2$	Intercept	Tree Species				Tree Species Richness
				Beech	Oak	Douglas-Fir	Norway Spruce	
Species Richness	64	–	2.29 $\pm$ 0.04					
K (g·kg <sup>-1</sup> )	63	0.912		28.22 $\pm$ 2.52 <sup>b</sup>	28.98 $\pm$ 2.88 <sup>b</sup>	41.08 $\pm$ 2.52 <sup>a</sup>	29.96 $\pm$ 2.61 <sup>b</sup>	
Ca (g·kg <sup>-1</sup> )	63	–	7.62 $\pm$ 0.50					
Mg (g·kg <sup>-1</sup> )	63	0.908		1.54 $\pm$ 0.14 <sup>b</sup>	1.64 $\pm$ 0.14 <sup>ab</sup>	2.10 $\pm$ 0.14 <sup>a</sup>	1.69 $\pm$ 0.14 <sup>ab</sup>	
P (g·kg <sup>-1</sup> )	63	–	3.59 $\pm$ 0.14					
C (%)	62	–	41.38 $\pm$ 0.65					
N (%)	62	0.936		1.78 $\pm$ 0.12 <sup>ab</sup>	1.75 $\pm$ 0.12 <sup>ab</sup>	2.16 $\pm$ 0.12 <sup>a</sup>	1.63 $\pm$ 0.12 <sup>b</sup>	
C:N	62	0.967		22.80 $\pm$ 1.13 <sup>bc</sup>	24.99 $\pm$ 1.13 <sup>ab</sup>	20.77 $\pm$ 1.17 <sup>c</sup>	26.10 $\pm$ 1.17 <sup>a</sup>	
N:P	62	–	5.35 $\pm$ 0.17					
Gram Biomass (g·m <sup>-2</sup> )	63	0.748		74.78 $\pm$ 18.65 <sup>a</sup>	90.17 $\pm$ 18.09 <sup>a</sup>	53.20 $\pm$ 18.09 <sup>ab</sup>	31.40 $\pm$ 18.30 <sup>b</sup>	28.62 $\pm$ 7.94
Herb Biomass (g·m <sup>-2</sup> )	63	–	40.43 $\pm$ 7.54					
Total Biomass (g·m <sup>-2</sup> )	63	0.841		118.27 $\pm$ 19.59 <sup>a</sup>	130.79 $\pm$ 19.00 <sup>a</sup>	99.22 $\pm$ 19.00 <sup>ab</sup>	43.77 $\pm$ 19.223 <sup>b</sup>	32.11 $\pm$ 8.33

layer, explaining the significant compositional shift between 2004 and 2010. Trees generally have a species-specific influence on environmental conditions that may induce differences in herb layer composition. However, the compositional turnover between 2004 and 2010 and the composition of the herb layer in 2004 and 2010 based on presence/absence data (using the Lennon distance measure) showed no significant influence of the planted tree species. The Lennon distance measure only takes into account pure species turnover, while ignoring other compositional differences between vegetation communities growing under different tree species, such as nestedness and other richness differences (Baselga 2010). Nestedness is a pattern that would occur, for instance, if the herb layer composition under a particular tree species is a complete subset of the vegetation assemblage under another tree species (cf. Ulrich & Gotelli 2007). Hence, the use of the Lennon distance measure may have underestimated the overall variation in herb layer community composition among tree species. Meanwhile, in 2010, compositional dissimilarities in the herb layer based on cover data (using the Bray-Curtis distance measure) showed a slightly significant difference between tree species, indicating that the tree species identity effects already induced small shifts in environmental conditions (e.g. relative light availability was lower for Douglas-fir) and therefore in the abundances of the different herb layer species. We found no significant difference in quadrat-level herb layer species richness between tree species. This contradicts the results of Skov (1997) and Emmer et al. (1998) who found that

conifers are less favourable to herb layer diversity than deciduous trees due to deterioration of growing conditions. Brunet et al. (1996) also reported higher herb layer species richness in stands of oak compared to beech. Our contrasting results might be due to the young age of the experiment and to the fact that the reaction of the herb layer may lag behind on environmental changes (Thomas et al. 1999). We expect the environmental impact of the planted trees to increase further as they grow older, which might lead to the loss of some species and the establishment of others in the longer term.

Indicator species analysis resulted in some indicators for beech, Douglas-fir and Norway spruce quadrats. All indicator species point at high light availability, combined with intermediate soil acidity and humidity, but with high soil fertility for Douglas-fir, intermediate soil fertility for Norway spruce and low soil fertility for beech. Looking at the difference in mean Ellenberg R between 2004 and 2010, none of the tree species induced significantly lower values. Hence, there was not yet a significantly lower share of herb layer species sensitive to soil acidification and/or a higher share of acido-tolerant species during stand development, but this difference might occur in a later phase. Namely, Calvaruso et al. (2011) saw a soil acidifying effect of beech, while Ewald (2000), Langenbruch et al. (2012) and Verstraeten et al. (2013) observed this effect in the presence of spruce, and Finch & Szumelda (2007) for Douglas-fir. Aubert et al. (2004) saw an increasing occurrence of acidophilous species during beech stand maturation, while Thomaes et al. (2012) concluded the same for oak stands.



**Fig. 4.** Influence of tree species richness on herb layer biomass and species richness. Plot level herb layer total biomass (a) and species richness (b) as a function of tree species richness at the BIOTREE tree diversity experiment in 2010 (mean  $\pm$  SE; *P*-values indicate the significance of Pearson's product moment correlation; *n* indicates the number of observations used for calculation).

Augusto et al. (2003) concluded that soils under coniferous species were more acidic than soils under hardwoods. The negligible tree species identity effects on Ellenberg L values in 2010 contrast with the difference in relative light availability between the tree species (lower values for Douglas-fir). The relation between light regime and herb layer might be better explained by past light conditions, as the reaction of the herb layer species pool lags behind (Thomas et al. 1999): BIOTREE Kaltborn is located on former grassland that was characterized by rather homogeneous and high light availability for the herb layer. The fact that the difference in relative light availability between tree species was still relatively small might be due to incomplete crown closure in this young experiment, especially for the deciduous species beech and oak. Vegetation quadrats were located at the centre of the patch in between four trees, where a considerable amount of incident sunlight reached the vegetation quadrats through gaps between the individual crowns, independent of the tree species. For the same reason, the effects of potential differences in stem flow or root competition between tree species on the herb layer community may have been lowered.

The coniferous species Douglas-fir and especially Norway spruce had a negative impact on total herb layer and graminoid biomass. Kembel & Dale (2006) also noticed that vascular plant cover, which is related to herb layer biomass, was generally positively associated with decidu-

ous tree cover and negatively associated with coniferous tree cover. Saetre et al. (1997) found that admixture with birch increased herb layer cover compared to pure spruce stands. The negative effect of coniferous species on herb layer biomass can be due to the higher Al concentrations and lower pH in the soil (Menyailo et al. 2002; Augusto et al. 2003), although Ellenberg R values did not confirm this negative effect of coniferous species on soil pH at BIOTREE. These effects are often reinforced by the low light transmittance towards the herb layer through most coniferous species (Chávez & Macdonald 2010). We already observed this lower light availability for Douglas-fir in 2010. The higher biomass of graminoids compared to herbs can be assigned to the history of the site (dominance of graminoid species in grassland) and the young age of the experiment. During stand maturation a typical forest climate will develop that will cause changes in the present graminoid species, both in composition and biomass, as was found by Buscardo et al. (2008). The tree species also seemed to affect the chemical composition of the above-ground biomass, with higher K, Mg and N concentrations and lower C:N ratio in the total biomass sample under Douglas-fir. Nutrients stored in the herb layer biomass are released during decomposition of herb layer foliage. Tree species thus plays a significant role in cycles of important plant nutrients. The tree species identity effect on nutrient concentrations cannot be explained by intrinsic differences in chemical composition between herb layer species (e.g. Santruckova et al. 2006), as dissimilarities in herb layer composition between tree species were not significant. Lower light availability, such as under Douglas-fir, affects leaf growth, resulting in leaves with a higher SLA (i.e. thinner but bigger leaves; McIntyre & Strauss 2014) and higher total chlorophyll content (Perrin & Mitchell 2013), in order to capture more light. These structural changes imply an increase in the concentration of the chemical constituents to allow adequate photosynthesis, which may explain the higher K, Mg and N concentrations in the herb layer biomass under Douglas-fir (e.g. Laing et al. 2000; Zhao et al. 2001). The higher nutrient concentrations in the herb layer biomass under Douglas-fir may also be due to the stronger effect of Douglas-fir on dieback of the herb layer biomass, mineral weathering and soil organic matter compared to the other tree species, leading to higher availability and therefore higher uptake of soil nutrients, or to reduced competition for nutrients due to the lower biomass (see above).

The presence of multiple tree species in a mixed forest stand, ordered in a chessboard pattern of monospecific patches, may lead to a heterogeneous distribution of resources (Yankelevich et al. 2006). According to the resource heterogeneity hypothesis, this may induce compositional dissimilarity in the herb layer between patches,

and hence a higher herb layer species richness at the stand level. For example, a mosaic of patches composed of trees species with different crown densities supports the co-existence of both shade-intolerant (early-successional) and shade-tolerant (late-successional) herb layer species (Chávez & Macdonald 2010). Mölder et al. (2008) found that the herb layer of forest stands with species-rich overstories was more diverse than the herb layer of beech-dominated stands. Ingerpuu et al. (2003) also found that the number of herb layer species was significantly positively correlated with the species richness of the tree layer. At the BIOTREE experiment, the plot-level species richness of the herb layer slightly increased from monocultures towards three-species mixtures in 2010, although the difference was still not significant. The lack of a clear plot-level increase can be due to the young age of the experiment, and hence, the relatively small tree species identity effects on environmental conditions (confirmed by the lack of compositional differences in the herb layer between quadrats surrounded by different tree species). However, Both et al. (2011) also did not find a positive tree–herb layer diversity relation in a subtropical forest in China. Barbier et al. (2008) even found indications that monospecific stands can be more favourable to the herb layer diversity than two-species stands.

The effect of mixing tree species on ecosystem functioning, such as the production of herb layer biomass, is not always solely the result of tree species identity effects but may also partially reflect tree species richness effects. As there was no complete dilution at the BIOTREE experiment, the experimental set-up allowed analysing tree species identity and richness effects separately. Quadrat- and plot-level total and graminoid biomass showed an increase towards higher tree species richness. Species-rich tree layers induce a more variable environment, which may lead to better growth conditions (Vockenhuber et al. 2011) and therefore a higher biomass of the herb layer. Sapijanskas et al. (2013) suggested complementarity in below-ground resource uptake might occur, while the findings of Mölder et al. (2008) indicated that herb layer biomass was promoted under diverse tree layers by increased nutrient supply and base saturation. Moreover, according to Ball et al. (2008) decomposition may proceed faster in mixed litter layers, leading to better soil conditions (nutrient availability, soil acidity), which may increase the herb layer biomass. However, BIOTREE plots were relatively young and tree litter was not yet spread far into neighbouring patches of a different tree species within the same plot. The impact of higher litter decomposition rates on herb layer biomass in mixed plots was therefore probably negligible. The positive relation with tree species richness must be related to another (unknown) factor(s).

Although the experiment was relatively young, significant tree species identity effects on herb layer composition and biomass and nutrient concentrations and ratios in the herb layer above-ground biomass could already be discerned. Moreover, higher tree species richness led to a small (insignificant) increase of plot-level herb layer species richness and higher graminoid and total biomass of the herb layer. Duffy (2009) concluded that small-scale, short-term experiments such as BIOTREE might underestimate the impact of tree diversity. Namely, environmental heterogeneity increases at larger spatial scales and with greater temporal fluctuations, and creates opportunities for species to exploit more niches (Dimitrakopoulos & Schmid 2004; Cardinale et al. 2007, 2012). Relations between tree species richness and herb layer diversity were indeed rather weak 6 yr after the BIOTREE experiment was started. So far, the young tree age, combined with the planting design using small monospecific patches instead of mixing tree species tree by tree, only allowed interactions between trees species at the borders between these patches. We expect the relations between tree and herb layer to become stronger through time as trees will grow higher and will also exert more influence on neighbouring patches. Apart from tree species identity effects and additive tree species richness effects as a result of resource heterogeneity, non-additive tree species richness effects will probably also appear. We therefore recommend re-monitoring the BIOTREE plots once a mature development phase has been reached.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Herb layer species present in 2004 and 2010.

**Appendix S2.** Indicator species as a function of the tree species surrounding the vegetation quadrat.

**Appendix S3.** Quadrat-level relative light availability as a function of the tree species surrounding the vegetation quadrat.