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Research article

Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest

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A B S T R A C T

In temperate deciduous forests, the herb layer contributes most to total vascular plant species richness. The diversity of the tree layer can influence herb layer diversity by modifying resource availability and environmental conditions relevant to herb layer plants. Here, we explore the relationship between tree layer diversity and herb layer species richness and cover. Also, we address the question how different environmental factors that are potentially modified by the tree layer influence herb layer characteristics. Our study area is located in the Hainich National Park, one of the largest continuous stretches of broad-leaved deciduous forest in Central Europe. We recorded herb and tree layer composition on 79 plots selected along a tree diversity gradient ranging from two to nine tree species. In addition, canopy cover, soil pH, mass of the humus layer, soil C:N ratio, soil moisture and distance to the forest edge were determined. We used generalized least square models to analyse effects of tree diversity, environmental variables, and spatial plot positions on herb layer species richness and cover. Species richness and cover of the herb layer increased with increasing tree diversity. In addition, both species richness and cover showed a negative response to increasing canopy cover and mass of the humus layer. Herb layer species richness was also positively related to increasing soil pH and the distance to the forest edge. The proportion of forbs increased with increasing tree diversity, whereas the proportion of tree saplings decreased and the proportion of graminoids was not affected. The proportion of true forest species increased with increasing canopy cover. We conclude that forest stands with a high tree diversity feature a more diverse herb layer and a higher herb cover. Furthermore, the environmental variables humus layer mass, light availability and pH also strongly affect herb layer species richness and cover.

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Introduction

In temperate deciduous forests, the herb layer holds most of the total vascular plant diversity, comprising up to 90% of all plant species of the forest (Whigham, 2004; Gilliam, 2007). Although the herb layer makes up only a small proportion of the total forest biomass, it contributes substantially to energy flow and nutrient cycling (Yarie, 1980; Gilliam, 2007). Spring ephemeral herbs can act as nutrient sinks during spring when nutrient uptake by trees is low and deciduous forests experience the annual maximal loss of nutri-

ents due to leaching (Peterson and Rolfe, 1982; Mabry et al., 2008). Herb foliage has a higher nutrient content than tree foliage and decomposes twice as rapidly (Muller, 2003), resulting in increased nutrient cycling (Gilliam, 2007).

Higher tree layer diversity might enhance herb layer diversity either by increasing environmental heterogeneity (Beatty, 2003) or by creating environmental conditions that are favourable to a greater number of herb species. While linkages between the diversity of the herb and tree layer have been commonly reported (Gilliam, 2007; Barbier et al., 2008), most studies so far compared herb layer diversity between forest types with only a few dominant tree species or between different monospecific stands, in particular conifer vs. broad-leaved forests. Little is known on how the diversity of the tree layer affects herb layer diversity across a wider gradient of broad-leaved tree species richness (Scherer-

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Lorenzen et al., 2007), though some results point towards a positive relationship between tree and herb layer diversity (Barbier et al., 2008; Mölder et al., 2008). In Europe, national forest programmes increasingly aim at enhancing forest biological diversity; however, research on ecosystem consequences of these biodiversity changes is still in its infancy.

A number of factors have been identified as determinants of herb layer diversity, for instance soil pH (Borchsenius et al., 2004; Hofmeister et al., 2009), nutrient availability (Small and McCarthy, 2005; van Calster et al., 2008), soil moisture (Qian et al., 1997; Lenière and Houle, 2006), mass of the litter layer (Gazol and Ibáñez, 2009; Kooijman, 2010), light availability (Härdtle et al., 2003; Tinya et al., 2009), and distance to the forest edge (Harper et al., 2005; Gonzalez et al., 2009). Changes in tree layer diversity can modify these factors because tree species differ in canopy structure, litter quality, and physiological characteristics (van Oijen et al., 2005; Guckland et al., 2009; Jacob et al., 2009; Wulf and Naaf, 2009). In Central Europe, broad-leaved forests are usually dominated by *Fagus sylvatica* L., a highly competitive tree species characterized by crowns with low light transmissibility and low-degradable litter with an acidifying effect on the soil (Ellenberg and Leuschner, 2010; Neirynck et al., 2000). Forests with high tree diversity show lower proportions of *F. sylvatica* and an increase in other broad-leaved tree species and might therefore be more suitable to a range of herb layer plants which do not tolerate conditions created by *F. sylvatica* (Mölder et al., 2008).

Here, we use a near-natural temperate deciduous forest system to study how tree diversity and environmental factors shape species richness and cover of the herb layer. We look separately at different plant functional groups and life forms to investigate group-specific responses. Furthermore, we analyse effects on the proportion of true forest species, because herbaceous species that are closely tied to forests may differ in their habitat requirements from plants that are only occasionally found under closed canopies (Burke et al., 2008). The Hainich National Park offers optimal conditions to study tree diversity effects; with its mixture of forest stands differing in tree diversity, it provides both the complexity of a natural forest ecosystem and a wide gradient in broad-leaved tree species diversity (Leuschner et al., 2009). We focus on the following questions:

(1) How are species richness and cover of the herb layer related to the diversity of the tree layer?
(2) Which environmental factors affect herb layer species richness and cover and what is their relative importance?
(3) How do the proportions of different plant functional groups and life forms respond to gradients of tree diversity and environmental variables?
(4) Which variables determine the proportion of true forest species in the herb layer?

Methods

Study area and study sites

We conducted our study in the Hainich National Park (Thuringia, Germany), near the village of Weberstedt (51°05′28″N, 10°31′24″E). The Hainich forest covers approximately 16,000 ha of wooded area, one of the largest continuous stretches of deciduous forest in Central Europe. The southern part of the Hainich forest has been subject to only very extensive management for over the past 40 years, becoming a military training ground in 1964 and a national park in 1997. Historic harvesting practises included coppicing systems and selective cutting (Mölder et al.,

2006). Some areas (for instance the Lindig location, see below) still feature structural characteristics of a coppice-with-standards forest. All investigated forest stands hold deciduous forest for at least 200 years (Mölder, 2009). With this level of stand continuity, they represent ancient forest stands as defined by Wulf (2003). The median age of the canopy trees does not differ widely between different parts of the study area (79–117 years, see Mölder, 2009; our plots are located in close vicinity to the larger plots described by Mölder). Climatic conditions are subatlantic with continental influence; the mean annual temperature is 7.7 °C, mean annual precipitation amounts to 630 mm (Gauer and Aldinger, 2005). The research area is situated at an elevation of approximately 350 m a.s.l. The predominant soil type is (stagnic) Luvisol developed from Triassic limestone as bedrock with partial loess cover (Leuschner et al., 2009).

The dominant tree species are *F. sylvatica* L., *Tilia platyphyllos* Scop., *Tilia cordata* Mill., and *Fraxinus excelsior* L. The species *Carpinus betulus* L., *Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Prunus avium* L., *Sorbus torminalis* (L.) Crantz, *Quercus robur* L., *Quercus petraea* Liebl. and *Ulmus glabra* Huds. are found less frequently. Dominant forest communities include the Galio odorati-Fagetum Sougnez et Thill 1959, the Hordelymo-Fagetum Kuhn 1937, and the Stellario-Carpinetum Oberd. 1957 (Mölder et al., 2006). Due to historic differences in forest ownership and management, adjacent forest stands show different levels of tree diversity while still exhibiting comparable climatic and edaphic conditions (Leuschner et al., 2009).

In spring 2008, we selected $N = 100$ plots of differing tree diversity ("tree clusters"; see Leuschner et al., 2009) arranged in two locations (each $N = 50$), Lindig and Thiemsburg (distance between locations approximately 1.5 km) (Appendix A). Plot selection was based on a priori combinations of tree species (Leuschner et al., 2009; not considered here). Plots were circular in shape (radius 20 m), and plot centres were on average 60 m apart. 21 plots were excluded because they were surrounded by deer fences, leaving 36 plots at the Thiemsburg location, and 43 plots at the Lindig location (see Appendix A). Distances from the plot centres to the nearest forest edge were determined using maps and subsequently used for analyses. The mean distance to the forest edge was 387 m; excluding the plot with the smallest distance to the edge (17 m) from analyses did not change results substantially. All plots were located at least 20 m away from forest paths, a distance that should be sufficient to avoid effects on the herb layer since it has been shown that the impact of forest paths on the vegetation extends less than 5–10 m into the surrounding forest (e.g. Avon et al., 2010). As the study area is located in a National Park, visitors are not allowed to walk off-track. Triassic limestone (Upper Muschelkalk) forms the soil parent material for all plots (Preußische Geologische Landesanstalt, 1905). To establish that initial soil properties were comparable between plots with different tree diversities, we tested for correlations between soil properties (pH, C:N content, clay content) of deeper soil horizons (10–20 cm depth) that are rarely modified by tree species (Augusto et al., 2003; Hagen-Thorn et al., 2004). C:N ratio and clay content of the deeper soil horizon were not correlated with tree diversity (C:N ratio: Spearman's rank correlation coefficient = 0.05, $P = 0.69$; clay content: Spearman's rank correlation coefficient = 0.11, $P = 0.34$), while pH showed only a weak positive correlation (Spearman's rank correlation coefficient = 0.28, $P = 0.01$).

Herb layer measurements

Herb layer species richness and cover were recorded within two 1 m × 1 m subplots near the plot centre in June 2008 and 2009. Vegetation survey plots of 1 m² area have been previously used

in studies on herb layer diversity patterns (van Oijen et al., 2005; Macdonald and Fenniak, 2007; Takafumi and Hiura, 2009) and are well suited to this type of studies since linkages between overstorey and understorey are often most easily detectable at small scales (Gilliam and Roberts, 2003). We estimated percentage cover of each vascular plant species present. All plants with a height <70 cm were considered as belonging to the herb layer. The herb layer species richness per plot was calculated as the cumulative sum of different herb layer species over subplots and years. Mean cover values per subplot and year were used to calculate herb layer cover.

We assigned herb layer plant species to ecological groups based on three criteria: (i) functional group (forbs, graminoids, tree saplings, shrubs, vines, ferns), (ii) life form (phanerophytes, chamaephytes, hemicryptophytes, geophytes, therophytes; following Klotz et al., 2002), and (iii) forest specialisation (true forest species that are closely tied to closed forests vs. indifferent species, following Schmidt et al., 2003) (Appendix B). Tree saplings and vines were not included in the analysis of forest specialisation. Nomenclature of vascular plants follows Wisskirchen and Haeupler (1998).

As herb species richness was recorded in summer only, purely vernal herb species were not considered in this study. However, a comparison between 40 plots for which both spring and summer vegetation surveys were conducted in 2009 revealed a high correlation between the species richness found in spring and in summer (Pearson's $r = 0.97$). Therefore, we are confident that herb species richness data obtained in summer provides adequate information about overall herb species richness within the plots.

Tree layer measurements

To measure tree diversity on the plots, we recorded species and diameter at breast height (dbh) of all trees with a dbh >6 cm that were present on the plot (circle with 20 m radius, area: 1257 m^2) between April and August 2009. Tree diversity was expressed by the Shannon–Wiener diversity index (H') based on relative stem area, which incorporates species richness as well as abundances of species (Magurran, 2004). The number of broad-leaved tree species per plot ranged from 2 to 9 species. Dominant species were *F. sylvatica* (Thiemsburg: 48%, Lindig 5%), *Tilia* sp. (Thiemsburg: 16%, Lindig: 44%) and *F. excelsior* (Thiemsburg: 20%, Lindig 23%). No conifers were present. *T. cordata*/*T. platyphyllos* and *Q. robur*/*Q. petraea* were recorded on genus level as these species could not be reliably distinguished in the field.

Measurement of abiotic variables

Canopy cover was used as an indirect measure of the light regime on our study plots (Jennings et al., 1999). All plots were scanned during summer 2008 with a Z + F Imager 5006 terrestrial laser scanner (Zoller und Fröhlich, Wangen, Germany) in a multiple scan design with 5–12 scans per plot, with the laser scanner positioned on the forest floor. The scans were aligned to each other based on 24 artificial targets placed in the plot and merged to only one single 3D-point cloud representing the plot. The virtual space above the plot was then subdivided into volume units of 5 cm × 5 cm × 5 cm, so-called voxels. If a voxel contained one or more points from the 3D-point cloud, it was considered as "filled". Canopy cover was calculated based on the ratio of the area covered by the projection of the filled voxels onto the ground to the total area (20 m × 20 m around the centre of the plot).

The volumetric soil water content was measured with mobile TDR (Time Domain Reflectometry) probes, connected to a circuit analyzer and vertically inserted into the soil to a depth of 30 cm. The soil moisture content was collected at four random locations near

the plot centre in April, July, early and late August, and September 2009. To account for the natural heterogeneity of the soils in the research area, a soil specific calibration was conducted in the laboratory on eight undisturbed soil samples, largely following the procedure described in the study by Veldkamp and O'Brien (2000). As measurements from the five sampling dates were highly correlated (Pearson's $r = 0.83$–0.92), we used mean values across sampling dates for further analyses.

Soil sampling took place in May 2008. To assess humus layer mass per unit area, a soil sample (20 cm diameter, 0–5 cm depth of mineral soil) was taken at the plot centre. The humus layer (including litter) was separated from the mineral soil and dried at 60 °C until constant weight. The stock of humus layer in kg m^{-2} was calculated as the quotient of dry matter divided by the sampling area. To record pH and C:N ratio, we took soil samples (6.4 cm diameter, 0–10 cm depth) at three locations near the plot centre. The soil samples were dried at 40 °C until constant weight and passed through a 2 mm sieve. Soil pH was measured in a suspension with H_2O_{bidest} (10 g of soil, 25 ml of H_2O). Organic carbon and total nitrogen were measured from the mineral soil by an automated C and N analyser (Heraeus Elementar Vario EL, Hanau, Germany) after being ground and weighted into tin ships (all samples were free of carbonates); subsequently, the C:N ratio was calculated.

Explanatory variables are summarized in Table 1.

Data analysis

We analysed species richness and cover of the total herb layer as well as cover and relative proportion of forbs, graminoids and tree saplings separately using generalized least square (gls) models fit by maximum likelihood (Pinheiro and Bates, 2000). Proportions of true forest species and different plant life forms were also analysed using gls models. Explanatory variables were weakly to moderately correlated, with pH and soil moisture showing the strongest correlation (Spearman's rank correlation coefficient = 0.59). All other explanatory variables had a Spearman rank correlation coefficient <0.5. We did not include the proportion of *F. sylvatica*, the most dominant tree species, into our main analyses because it was strongly correlated with several environmental variables. However, we present linear models containing only tree diversity and the proportion of *F. sylvatica* as explanatory variables in Appendix C so that the importance of the species identity effect of *F. sylvatica* can be evaluated. Data on percentage cover and species richness were arcsine square-root and log transformed, respectively. All explanatory variables were standardized to zero mean and unit variance before analyses. Tree saplings were excluded from the herb layer data for analysis of total herb layer species richness and cover because these species are not independent from the explanatory variable "tree layer diversity". Diagnostic plots were used to check for homoscedasticity, normality of errors, and outliers.

We tested for spatial autocorrelation in our analyses by plotting semivariograms of the residuals of our full models (Appendix D). Semivariograms show how quickly spatial autocorrelation falls off with increasing distance. If semivariograms indicated spatial autocorrelation, we corrected for the spatial correlation structure of the errors by including a spatial correlation parameter into our models that incorporates the x/y coordinates of the plots (Pinheiro and Bates, 2000).

To incorporate the considerable uncertainty inherent in selecting one single "best" model, we applied multi-model inference and model averaging, a method where statistical inference is based on an entire set of models (Burnham and Anderson, 2002). Based on a full model that included all explanatory variables as main effects, models with all combinations of explanatory variables were fitted and ranked according to their AICc values (Akaike's Information

Table 1
Summary statistics (mean, standard deviation, range) and description of explanatory variables. SD = standard deviation. Units of variables indicated in brackets.

Variable name	Description	Mean	SD	Minimum	Maximum
Location	Locations Lindig and Thiemsburg, factor with two levels	–	–	–	–
Tree diversity	Shannon–Wiener diversity index H' of trees	1.28	0.33	0.27	2
Distance forest edge	Distance to the nearest forest edge (m)	387	212	17	830
Canopy cover	Area of ground covered by vertical projection of canopy, arcsine square-root transformed (%)	90.7	4.2	69.1	96.4
Humus layer mass	Mass of the humus layer per unit area (kg m^{-2})	0.05	0.04	0.002	0.18
pH	Soil pH in depth of 0–10 cm	5.35	0.65	4.05	6.98
C:N ratio	Carbon-to-nitrogen ratio of soil in depth of 0–10 cm	13.72	0.99	11.88	18.36
Soil moisture	Volumetric soil water content (%)	32.71	2.84	17.88	54.69

Criterion, corrected for small sample sizes, Burnham and Anderson, 2002). First-order interactions with location and quadratic terms of explanatory variables were included in the full model if indicated by previous data exploration. We calculated Akaike weights (AICcw) and the differences in AICc (ΔAICc) for all models. ΔAICc represents the differences in AICc between the best model and the remaining models; the AICcw shows the likelihood of a certain model being the best in a set of models, given the data (Burnham and Anderson, 2002). Models with a ΔAICc ≤ 2 entered the set of best models. From this set of top models, we calculated model averaged parameter estimates and unconditional standard errors weighted by model AICcw (Burnham and Anderson, 2002; Wielgoss et al., 2010). To determine the relative importance of explanatory variables, we used $\sum$AICcw, the sum of Akaike weights of the set of top models in which the variable appeared. Variables with a larger value of $\sum$AICcw (which varies between 0 and 1) are considered to be more important since variables with $\sum$AICcw values close to 1 appear in all well-supported models.

All analyses were carried out using R, version 2.12.0 (R Development Core Team, 2009). Model averaging was carried out with the MuMIn package (version 0.13.17). Information about models (AICc, ΔAICc, AICcw) included in the top set of models for each separate analysis can be found in Appendix E.

Results

Species richness and cover of total herb layer

In total, 74 different plant species were recorded in the herb layer during this study (Appendix B). Plant species richness of the herb layer varied between 1 and 27 species per plot, with a mean ± standard deviation of 11 ± 6 species (including tree saplings: 2–32 species, mean = 15 ± 6). The cover of the herb layer ranged from 0.1 to 56.8% with a mean of 16.7 ± 12.4% (including tree saplings: 3–61.7%, mean = 26.3 ± 4.3%).
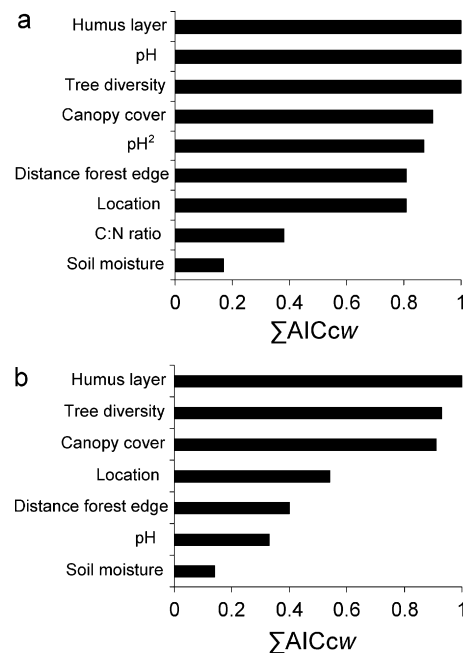
The species richness of the herb layer increased with increasing tree diversity (Fig. 1, Table 2). Herb layer species richness was also positively related to the distance from forest edge, while it decreased with increasing humus layer mass and canopy cover. Soil pH and herb layer species richness showed a positive relationship. The quadratic pH term received high support as well (Table 2), indicating a hump-shaped relationship between soil pH and herb layer species. Humus layer mass, pH and tree diversity had the highest sum of Akaike weights ($\sum$AICcw) and therefore the highest importance in explaining species richness of the herb layer (Fig. 2a). Canopy cover (0.90), distance to the forest edge (0.81) and location (0.81) also received high $\sum$AICcw values, while C/N ratio (0.38) and soil moisture (0.17) were of low importance. In a separate analysis with only tree diversity and the proportion of *F. sylvatica* as explanatory variables, the model including both variables had the best explanatory power (lowest AICc) (Appendix C).

Herb layer cover increased with increasing tree diversity, whereas canopy cover and humus layer mass had a negative influ-
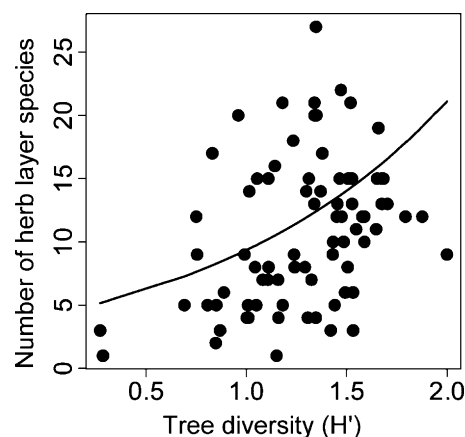
Fig. 1. Relationship between tree diversity (Shannon–Wiener index H') and herb layer species richness on 79 study plots in the Hainich National Park. The line shows the prediction based on model averaged estimates (Table 2), points are observations.

ence. Humus layer mass had the highest $\sum$AICcw (1), followed by tree diversity (0.93) and canopy cover (0.91) (Fig. 2b). There was weaker evidence for an effect of location (0.54) or distance

Fig. 2. Relative importance of environmental variables in explaining variation in (a) species richness and (b) cover of the herb layer. Variables are ranked in order of the sum of their Akaike weights ($\sum$AICcw). Tree saplings were excluded from analysis of total herb layer species richness and cover because these species are not independent from the explanatory variable "tree diversity". pH^2 denotes the quadratic term of the variable pH.

Table 2
Multi-model averaged coefficients and unconditional standard errors of parameters determining herb layer species richness and cover as well as the proportion of true forest species. ":" denotes a two-way interaction. Treatment contrasts were used: (Intercept) represents the mean for "Thiemsburg"; parameter estimates for categorical main effects are differences between means; parameter estimates for numeric main effects and interaction terms are differences between slopes. Negative coefficients for quadratic terms indicate hump-shaped relationships. Herb layer species richness was log transformed, herb layer cover arcsine square-root transformed. All numeric explanatory variables were standardized to zero mean and unit variance.

	Total herb layer species richness	Total herb layer cover	Proportion of forest species
(Intercept)	2.46 ± 0.151	0.415 ± 0.046	0.571 ± 0.068
Location Thiemsburg	-0.402 ± 0.272	-0.071 ± 0.088	0.019 ± 0.082
Tree diversity	0.266 ± 0.068	0.036 ± 0.02	0.017 ± 0.027
Tree diversity^2	–	–	0.014 ± 0.017
Canopy cover	-0.118 ± 0.07	-0.034 ± 0.02	0.046 ± 0.021
Humus layer	-0.221 ± 0.09	-0.064 ± 0.022	-0.079 ± 0.026
pH	0.228 ± 0.092	0.008 ± 0.014	0.007 ± 0.012
pH^2	-0.086 ± 0.057	–	–
Distance forest edge	0.242 ± 0.159	0.03 ± 0.041	-0.037 ± 0.076
C:N ratio	0.047 ± 0.069	–	-0.005 ± 0.009
Soil moisture	-0.019 ± 0.037	0.002 ± 0.005	0.001 ± 0.003
Location:tree diversity	–	–	-0.021 ± 0.035
Location:distance forest edge	–	–	0.183 ± 0.105

Table 3
Multi-model averaged coefficients and unconditional standard errors of parameters determining proportion and cover of forbs, graminoids and tree saplings. ":" denotes a two-way interaction. Treatment contrasts were used: (Intercept) represents the mean for "Thiemsburg"; parameter estimates for categorical main effects are differences between means; parameter estimates for numeric main effects and interaction terms are differences between slopes. The response variable "cover" was arcsine square-root transformed for all functional groups. All numeric explanatory variables were standardized to zero mean and unit variance.

	Forbs		Graminoids		Tree saplings	
	Proportion	Cover	Proportion	Cover	Proportion	Cover
(Intercept)	0.498 ± 0.029	0.344 ± 0.032	0.153 ± 0.024	0.195 ± 0.027	0.314 ± 0.032	0.343 ± 0.041
Location Thiemsburg	-0.009 ± 0.019	-0.029 ± 0.045	-0.028 ± 0.042	-0.069 ± 0.037	0.038 ± 0.056	-0.112 ± 0.079
Tree diversity	0.059 ± 0.021	0.048 ± 0.02	-0.005 ± 0.009	–	-0.048 ± 0.016	-0.002 ± 0.004
Canopy cover	–	-0.042 ± 0.02	0.001 ± 0.002	-0.016 ± 0.012	0.001 ± 0.003	–
Humus layer	-0.004 ± 0.009	-0.033 ± 0.025	-0.027 ± 0.018	-0.002 ± 0.004	0.052 ± 0.018	–
pH	0.073 ± 0.022	0.043 ± 0.019	-0.015 ± 0.015	–	-0.084 ± 0.021	-0.035 ± 0.015
Distance forest edge	-0.013 ± 0.021	–	0.032 ± 0.029	0.09 ± 0.031	-0.013 ± 0.022	0.063 ± 0.041
C/N ratio	-0.029 ± 0.023	–	0.001 ± 0.001	-0.002 ± 0.004	0.002 ± 0.004	0.003 ± 0.007
Soil moisture	-0.015 ± 0.022	–	–	–	0.006 ± 0.011	–
Location:distance forest edge	–	–	–	-0.099 ± 0.038	–	–
Location:canopy cover	–	0.014 ± 0.025	-0.004 ± 0.008	–	–	–
Location:pH	–	–	–	–	0.076 ± 0.029	–

to the forest edge (0.40). Soil pH (0.33) and soil moisture (0.14) received little support. The C:N ratio did not enter any models in the top set. When only tree diversity and the proportion of *F. sylvatica* were used as explanatory variables, the model containing only the proportion of *F. sylvatica* had the best fit (Appendix C).

Proportion and cover of functional groups

We focused our analyses on forbs (59.5% of all herb layer species), graminoids (16.2%), and tree saplings (14.9%), because ferns (4.1%), shrubs (4.1%), and vines (1.4%) did not contain sufficient species for analyses. The proportion of forbs as well as forb cover were positively influenced by tree diversity and pH (Table 3). Also, the proportion of forbs was negatively related to the C/N ratio, while the forb cover responded negatively to increasing canopy cover and humus layer. In contrast to forbs, relative proportion and cover of graminoids did not respond to tree diversity (Table 3). Proportion of graminoids increased with increasing distance to the forest edge and decreased with increasing pH and humus layer mass. Graminoid cover was negatively associated with canopy cover and also increased with distance to the forest edge, but only at the Lindig location. The proportion of tree saplings was negatively influenced by tree diversity and pH, but increased when the humus layer mass was higher (Table 3). Tree sapling cover responded negatively to increasing soil pH and positively to the distance to the forest edge.

Proportion of life forms

Hemicryptophytes represented 48.6% of all recorded herb layer species, followed by geophytes (21.6%), phanerophytes (20.3%), therophytes (2.7%) and chamaephytes (2.7%). Three species (4.1%) could not be assigned to a life form as they could not be determined to species level. Proportions of hemicryptophytes and geophytes increased with increasing tree diversity, while the proportion of phanerophytes decreased. Different life forms showed contrasting responses to environmental variables and the distance to the forest edge (Appendix F).

Proportion of true forest species

Plant species that were closely tied to the forest (K1.1 + K1.2, see Appendix B) made up 50% of all herb layer species recorded in the study area, while plants that occurred in forests as well as open vegetation (K2.1 + K2.2, see Appendix B) represented 42.9%. Four species could not be assigned to a group as they could not be determined to species level. On average, $67 \pm 18\%$ of the herb layer species per plot were true forest species. The proportion of true forest species increased with increasing canopy cover and decreased when the mass of the humus layer was high (Table 2). At the Thiemsburg location, the proportion of true forest species increased with increasing distance to the forest edge, while at the Lindig location, the proportion of true forest species was lower at greater distances to the forest edge.

Discussion

Effects of tree diversity

We have shown that forest stands with higher tree diversity were characterised by higher herb layer species richness and cover. Previous studies exploring tree diversity effects on the herb layer have shown mixed results: while some studies detected positive relationships between tree and herb layer diversity (Hicks, 1980; Ingerpuu et al., 2003; Mölder et al., 2008), others found no effect (Ewald, 2002; Borchsenius et al., 2004; Houle, 2007). Previously, many studies compared tree stands dominated by conifers to broad-leaved stands, often with the result of reduced herb species richness in the conifer stands (Berger and Puettmann, 2000; Hart and Chen, 2008). Other studies assessed tree diversity effects in forests with only a limited number of different tree species. In contrast, the present study allows inferences on tree diversity effects based on a wide diversity gradient in a purely broad-leaved forest setting.

A comparison between the different functional groups revealed that higher tree diversity went along with an increased proportion of forbs, while graminoids did not respond to tree layer diversity, and the proportion of tree saplings decreased. This might be caused by plant functional groups having different resource requirements and therefore exhibiting contrasting responses in reaction to environmental gradients (Weisberg et al., 2003; Graves et al., 2006; Tinya et al., 2009). High levels of tree diversity apparently create conditions that are more beneficial to forbs than to woody species of the herb layer. This is also shown by the decreasing proportion of phanerophytes with increasing tree diversity, whereas the other two dominant life forms, geophytes and hemicryptophytes, are enhanced.

Tree species can influence the herb layer by changing resource availability and environmental conditions in lower forest layers (Barbier et al., 2008). If dominant tree species create conditions that are unsuitable for many herbs, a more diverse canopy where the dominant tree species are less abundant might affect conditions on the ground in such a way that herb diversity and cover are enhanced. In the Hainich forest, secondary tree species occurring on more diverse sites include *F. excelsior*, *A. platyphyllos* and *Tilia* sp., species which may improve litter quality and light availability on the ground compared to stands dominated by *F. sylvatica* (Norden, 1994; Neirynck et al., 2000), thus leading to a higher diversity of herb layer species in these plots. The environmental heterogeneity hypothesis (Huston, 1994) could provide a further explanation for tree diversity effects, implying that a greater tree diversity may lead to higher small-scale heterogeneity of site conditions and consequently to a higher herb diversity. Though plausible, we cannot address this hypothesis as our vegetation survey plots were too small to reliably quantify spatial heterogeneity of environmental conditions.

Half of all plant species in the herb layer of our study area can be classified as species typical of closed forests. This agrees with findings in comparable unmanaged deciduous forests (Mölder et al., 2006) and indicates high continuity of forest cover (Graae and Sunde, 2000). Similar to Mölder et al. (2006), we did not find any evidence that tree diversity plays a substantial role in determining the proportion of true forest species.

Effects of environmental factors

The mass of the humus layer had particularly high importance in explaining overall species richness and cover of the herb layer. It decreased both species richness and cover. This finding agrees with previous studies which reported negative effects of litter depth, one element of the humus layer, on herb layer diversity or cover (Augusto et al., 2003; Mölder et al., 2008; Gazol and Ibáñez, 2009). A strongly developed humus layer might form a physical barrier that inhibits germination and emergence of herb layer plants (Sydes and Grime, 1981). While some herb layer plants have developed mechanisms to penetrate thick litter layers, others are suppressed (Dzwonko and Gawronski, 2002; Kooijman, 2010). Both forbs and grasses showed a negative response to strongly developed humus layers. In contrast, the proportion of tree saplings increased. Tree saplings might be better adapted to penetrate thick humus layers due to larger seed sizes (Dzwonko and Gawronski, 2002) and might experience less competition from forbs and graminoids in settings with a well-developed humus layer (Facelli and Pickett, 1991). Tree species differ in the decomposability of their litter, affecting the volume of the organic layer. For instance, *F. sylvatica* forms a thicker organic layer than other broad-leaved tree species (Wulf and Naaf, 2009; Jacob et al., 2010), which could contribute to lower herb species numbers on plots with a low tree diversity, i.e., plots dominated by *F. sylvatica.*

Herb layer species richness and cover increased with increasing pH. This finding agrees with numerous studies which documented a positive effect of pH on herb layer diversity (Lenière and Houle, 2006; Houle, 2007; Kooijman, 2010), with pH often emerging as the main driver of diversity and biomass in the herb layer. Many herb layer species cannot tolerate acidic conditions that lead to H^+ and Al^{3+} toxicity (Brunet et al., 1996). In addition, a higher pH may positively influence nutrient availability for plants: as many plants typical of beech forests preferentially take up NO_3^- as a nitrogen source, they prefer soils with neutral to slightly basic conditions where nitrifiers are active (Ellenberg and Leuschner, 2010; Härdtle et al., 2003). Comparing the different functional groups shows that proportion and cover of forbs responded positively to higher pH levels, while proportion and cover of tree saplings decreased. Forbs require more soil nutrients per unit biomass than tree saplings (Graves et al., 2006); therefore they might benefit more strongly than other functional groups from higher pH levels which favour a higher nutrient availability in the soil. The overstorey can influence soil pH by modifying the composition of stemflow- and throughfall water, the level of organic acid secretion via the roots and the composition of leaf litter (Augusto et al., 2002; Hagen-Thorn et al., 2004). *F. excelsior*, *A. platyphyllos* and *Tilia* sp., whose proportions increase with higher tree diversity, are known to produce less acidic topsoil than *F. sylvatica* (Aubert et al., 2004; Guckland et al., 2009).

High levels of canopy cover decreased herb layer species richness as well as cover of the total herb layer, forbs, and graminoids. Similarly, many studies emphasised the positive effect of greater light availability on herb layer diversity (Hart and Chen, 2008; Tinya et al., 2009; Härdtle et al., 2003; Hofmeister et al., 2009). However, others found no effect (Collins and Pickett, 1987; Augusto et al., 2003; Lenière and Houle, 2006). A higher light availability allows the presence of plant species which occur in forests as well as in grassland ecosystems and do not have special adaptations to the low light levels of the forest understorey. As long as these species do not outcompete forest specialists, a net increase in species richness and herb layer cover is to be expected. In accordance with Burke et al. (2008), we found an increasing proportion of true forest species with increasing canopy cover. The light environment in forest stands strongly depends on crown structure and density of the canopy trees (Jennings et al., 1999). In particular, dense canopies of *F. sylvatica* are known for low light transmittance compared to other broadleaved trees (Ellenberg and Leuschner, 2010).

Distance to the forest edge emerged as another important factor in explaining herb layer species richness. Depending on the type of forest edge considered and the local conditions of the study area, varying responses of the herb layer to the edge distance have been

observed, making it difficult to identify general patterns (Murcia, 1995; Harper et al., 2005). Proximity to the forest edge goes along with changes in biotic and abiotic conditions, potentially causing changes in plant community composition such as shifts towards a higher fraction of more light-demanding species and a restriction of forest interior species closer to the edge (Murcia, 1995; Gonzalez et al., 2010). Our results showed an increase of total herb layer species richness with increasing distance to the edge. Apparently, opportunist plant species that might benefit from lighter conditions closer to the forest edge did not play a major role, possibly because all plots except one were located more than 50 m away from the edge, which is commonly regarded as the maximum distance that edge effects penetrate into the forest (Murcia, 1995). We expected an increase in the proportion of true forest species with increasing distance to the edge; surprisingly, this was only confirmed in the Thiemsburg area. Differences in tree species composition between locations might explain this idiosyncratic response.

Soil moisture did not affect species richness and cover of the total herb layer or of any functional group. Across studies exploring drivers of herb layer diversity, soil moisture often seemed to play a minor role (Borchsenius et al., 2004; Gazol and Ibáñez, 2010; Ingerpuu et al., 2003), though some authors found a positive effect (Lenière and Houle, 2006; Qian et al., 1997; Härdtle et al., 2003). The overall soil moisture content in the Hainich forest may be high enough to rule out limiting effects on herb layer species. The composition of the tree layer can affect soil water availability by tree-species specific differences in the amount of non-intercepted rainwater (throughfall), stemflow and water taken up by the roots (Barbier et al., 2008).

We did not detect an influence of the C:N ratio on any herb layer attributes except the proportion of forbs. The C:N ratio can serve as an indicator of substrate quality and nitrogen limitation in forest soils (Currie, 1999; Small and McCarthy, 2005). Thus, it is not surprising that forbs, a functional group with pronounced nutrient requirements, showed a negative response to higher C:N ratios. Differences in litter composition between tree species can cause overstorey effects on soil C:N ratios (Augusto et al., 2002). The strength of the herb layer response to variations in the C:N ratio might be dependent on the overall N availability in different forest systems, on the form in which N is available and whether forests experience N limitation or rather excess N levels due to atmospheric deposition. Also, the C:N ratio spanned a rather narrow gradient in our study area and generally did not reach levels detrimental to plant growth.

Limitations

Due to the observational nature of this study we cannot rule out that both tree and herb layer diversity respond to pre-existing abiotic conditions, which could lead to a positive correlation between the diversity of the different forest layers irrespective of a causal relationship. Also, we are not able to disentangle pure tree diversity effects from effects of different tree species which vary in their abundance (dilution gradient, see Scherer-Lorenzen et al., 2007; Nadrowski et al., 2010). *F. sylvatica*, which strongly dominates the species-poor stands, might be mainly responsible for lower herb species numbers because it may create unfavourable soil and light conditions (Graae and Heskjaer, 1997; Barbier et al., 2008; Mölder et al., 2008). When only tree diversity and the proportion of *F. sylvatica* were used together as explanatory variables, the inclusion of tree diversity did still substantially improve the model explaining herb layer species richness, which suggests a tree diversity effect in addition to the species identity effect of *F. sylvatica*. However, for herb layer cover, the model containing the proportion of *F. syl-*

vatica alone received higher support. Future studies in forest types not dominated by *F. sylvatica*, but still containing a pronounced gradient of tree species richness, would help to shed light on the generality of our results. In spite of these limitations, we believe that comparative studies in established forests such as the Hainich National Park are important for understanding tree diversity effects because they provide representative conditions of (near) natural forest ecosystems at a mature stage. Experiments with planted tree stands often cannot provide the complexity of environmental conditions and processes occurring in old-growth forests, but do allow a better analyses of causal relationships since their design reduces collinearity between tree species diversity and other variables. Therefore, both experimental and observational studies should be used to investigate tree species diversity effects (Leuschner et al., 2009).

Forest management can have strong impacts on the plant species composition of the herb layer. Even though forest use was reduced to a minimum during the past 40 years in our study area, historic differences in forest management might not only have created stands with varying tree diversity, but might also have directly impacted understorey vegetation. This might partly explain contrasting herb layer responses to some environmental factors in the two study areas.

Conclusions

In the tree-diversity mosaic of the Hainich National Park, a positive association between diversity of the tree layer and species richness and cover of the herb layer was observed. However, the relative importance of tree diversity in explaining herb layer characteristics was equal or lower to the importance of certain environmental factors. While the variables humus layer mass, canopy cover, pH and distance to the forest edge were of high relative importance for explaining herb layer species richness and cover, soil moisture and the C:N ratio played a smaller role. We conclude that linkages between diversity patterns of tree and herb layer exist, but that controlled biodiversity experiments will be needed to disentangle diversity and species identity effects of the tree layer.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.02.004.

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