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When beech strikes back - How strict nature conservation reduces herb-layer diversity and productivity in Central European deciduous forests

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Abstract

Current nature conservation policy is going to alter the tree-layer composition of many Central European deciduous forests. As a consequence of ceasing silvicultural management, the competitive ecosystem engineer European beech (*Fagus sylvatica* L.) will spread and the proportion of secondary tree species will considerably decrease. Thus, changes can also be expected in herb-layer diversity, productivity and composition. To predict these changes, we analysed relationships between tree- and herb-layer diversity and composition along tree-diversity gradients in the Central German woodland areas of the Hainich National Park (unmanaged) and the Göttinger Wald (managed by close-to-nature forestry).

The flora of both study areas was dominated by typical forest species. In the Hainich, the herb-layer vegetation in beech-dominated stands was less diverse compared to stands richer in canopy species. Herb-layer productivity was also lower in beech-dominated stands. In the Göttinger Wald, herb-layer diversity and productivity were not related to tree-layer diversity and beech proportion, instead to the light transmissibility of the canopy layer. The different results can be explained by logging effects in the Göttinger Wald, which promoted the light factor as significant for herb-layer diversity and productivity. In the consistently darker stands of the Hainich, soil variables, particularly influenced by the ecosystem engineer beech, were decisive. Areas of high canopy diversity in the Hainich result from former management practices and can, in the future, be expected to decrease with the spread of beech.

We conclude that forest management cessation will result in decreasing herb-layer diversity and productivity in many Central European deciduous woodlands, especially in landscapes where historical management practices led to unnaturally low proportions of beech. The short-term consequence of management cessation is a loss of herb-layer diversity due to reduced light availability; in the long-term, herb-layer diversity is expected to decrease due to the expansion of beech.

If the key aim of nature conservation policy is to preserve and develop the typical diversity of near-natural beech forests, then a complete cessation of forest management can be advised. However, if the typical forest herb diversity of the semi-natural, century-old cultural landscape is to be maintained, close-to-nature forestry management is necessary.

Keywords:
Ecosystem engineer, Ecosystem functioning, *Fagus sylvatica*, Forest plant species, Silviculture, Unmanaged vs. managed forests

1. Introduction

Diversity relationships and interactions between forest strata are currently an important research topic (Leuschner et al., 2009; Nadrowski et al., 2010; Both et al., 2011; Martin et al. 2011; Bartels and Chen 2013). It is particularly crucial to study the effects of tree-layer composition variations on herb-layer vegetation, since herb-layer vegetation contributes significantly to the ecosystem functioning and biodiversity in forests (Augusto et al., 2003; Gilliam, 2007; McEwan and Muller, 2011). Productive and species-rich herb-layer vegetation can contain significant amounts of aboveground biomass and nutrients (Yarie, 1980; Schulze et al., 2009); during periods of high potential leaching, the temporary storage of elements by ground-layer herbs reduces nutrient losses into surface water (Mabry et al., 2008). Furthermore, many forest plant species are specially protected and high valued in nature conservation (Hermy et al., 1999; Jolls, 2003).

In Central European forests, the tree layer composition is heavily influenced by forestry. Without human activity, European beech (*Fagus sylvatica*) would be the dominating tree species, but silviculture also promotes a great number of other tree species (Heiri et al., 2009; Ellenberg and Leuschner, 2010). In deciduous forests on fertile soils this frequently led to the development of mixed stands, consisting of beech and economically more valuable broadleaved tree species (e.g., *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Prunus avium*), instead of pure beech stands (Spiecker et al., 2009). Also, historical woodland management practices, such as coppicing and coppicing with standards, altered the tree layer composition (Albert and Ammer, 2012; Altman et al., 2013). Due to the different traits of the canopy trees, the composition and diversity of the herb layer can be expected to change if *Fagus sylvatica* becomes more dominant in comparison to other deciduous tree species (Barbier et al., 2008). Presently in Germany, 16 % of the woodland area consists of beech-dominated stands (BMEL, 2014).

In general, the tree-layer composition has an effect on ground vegetation due to its influence on various ecosystem processes, e.g. nutrient cycles, light transmittance, and soil water supply (Augusto et al., 2003; Barbier et al., 2008; Chávez and Macdonald, 2011a; McEwan and

Muller, 2011). The chemical composition of tree leaf litter was particularly found to be a major factor influencing soil acidity and thereby nutrient stocks (Augusto et al., 2003; Langenbruch et al., 2012). Besides altered soil conditions, the light transmissibility of the canopy stratum was found to be another key factor affecting herb-layer diversity (Härdtle et al., 2003; Barbier et al., 2008) and productivity (Axmanová et al., 2012). Diffuse light is transmitted differently depending on the tree species, e.g., beech crowns transmit only a small proportion of daylight to the forest floor (Hagemeier, 2002).

In the future, nature conservation measures in Central Europe are expected to alter the tree-layer composition in many regions. In Germany, during the last two decades, the national parks of Hainich, Eifel and Kellerwald-Edersee have been established in landscapes with deciduous forests (Job, 2010). Additionally, there is a countrywide network of strict forest nature reserves (BLE, 2013). In the near future, there is expected to be an increasing amount of unmanaged forest stands, since the Federal Government of Germany has decided to ensure natural development on 5 % of German woodland by 2020 (Küchler-Krischun and Walter, 2007). Currently, 1.9 % of the German woodland area is designated to ensure long-term natural development (Wildmann et al., 2014). Following the cessation of silvicultural management, the competitive beech is expected to spread in many areas and to a great extend the proportions of secondary tree species will decrease (Heiri et al., 2009). As a consequence, the composition and diversity of the herb-layer vegetation can also be expected to change (Schmidt, 2005).

In order to predict these herb-layer vegetation changes, we analysed the herb-layer diversity, productivity and composition along a gradient from stands rich in canopy tree species down to pure beech stands (space-for-time substitution; Pickett, 1989) in two study areas with similar forest types and site conditions. Thereby, we investigated whether herb-layer diversity and productivity was related to canopy-layer diversity, with the aim of ascertaining possible causal mechanisms. Since it is important to know if varying (former) management practices result in different relationships between the canopy and the herb layer (Barbier et al., 2008; Durak, 2012), we studied unmanaged stands in the Hainich National Park on the one hand and multifunctional stands with a long tradition of close-to-nature forestry in the Göttinger Wald on the other. In addition, we analysed a 20-year time series on permanent plots from a strict forest nature reserve in the Göttinger Wald with regard to diversity changes in the tree- and in the herb-layer. To interpret the results with regard to conservation issues, the floristic composition of the study areas was also compared, since a close-to-nature composition of the herb layer is more important than maximum species richness, which may include many generalists (Hermy et al., 1999; Schmidt, 2009; Paillet et al., 2010; Boch et al., 2013).

Our research seeks to answer three main questions. When comparing deciduous stands in a national park without silvicultural management and in a multifunctional forest with a long tradition of close-to-nature forestry,

- Are there comparable relationships between tree-layer diversity and herb-layer diversity and productivity?
- Are there differences regarding the floristic composition and occurrence of forest plant species?
- Which biological, environmental, and anthropogenic factors and mechanisms can be held responsible for the observed relationships and differences?

2. Material and Methods

2.1 Tree-layer diversity gradients

2.1.1 Study areas and research site selection

The two study areas, Hainich National Park and Göttinger Wald, are located close to the centre of Germany (Fig. 1). They are about 65 km apart from one another. In each study area, 21 research sites represented a gradient from pure beech stands to mixed stands with the highest tree species richness occurring regularly in the region. The sites were selected by expert opinion after detailed preliminary studies and we sought to ensure that edaphic and climatic conditions were as comparable as possible among the sites of each gradient. This is very important, since sufficiently homogenous climate and soil conditions are crucial for the unbiased analysis of tree species effects on herb-layer vegetation (Barbier et al., 2008; Leuschner et al., 2009). Each research site was of 400 m² (20 m × 20 m) in size, characterised by consistent soil conditions, flat relief, a more or less homogeneous stand structure, and exhibited undisturbed herb-layer vegetation typical for the research area. The latter point is quite important, since, for instance, the deliberate avoidance of species-poor or even species-rich areas would cause bias in the subsequent analysis. The deciduous forests of both study areas have been in existence for at least 200 years (Preutenborbeck, 2009; Schmidt et al., 2009) and represent ancient woodland following the definition of Wulf (2003).

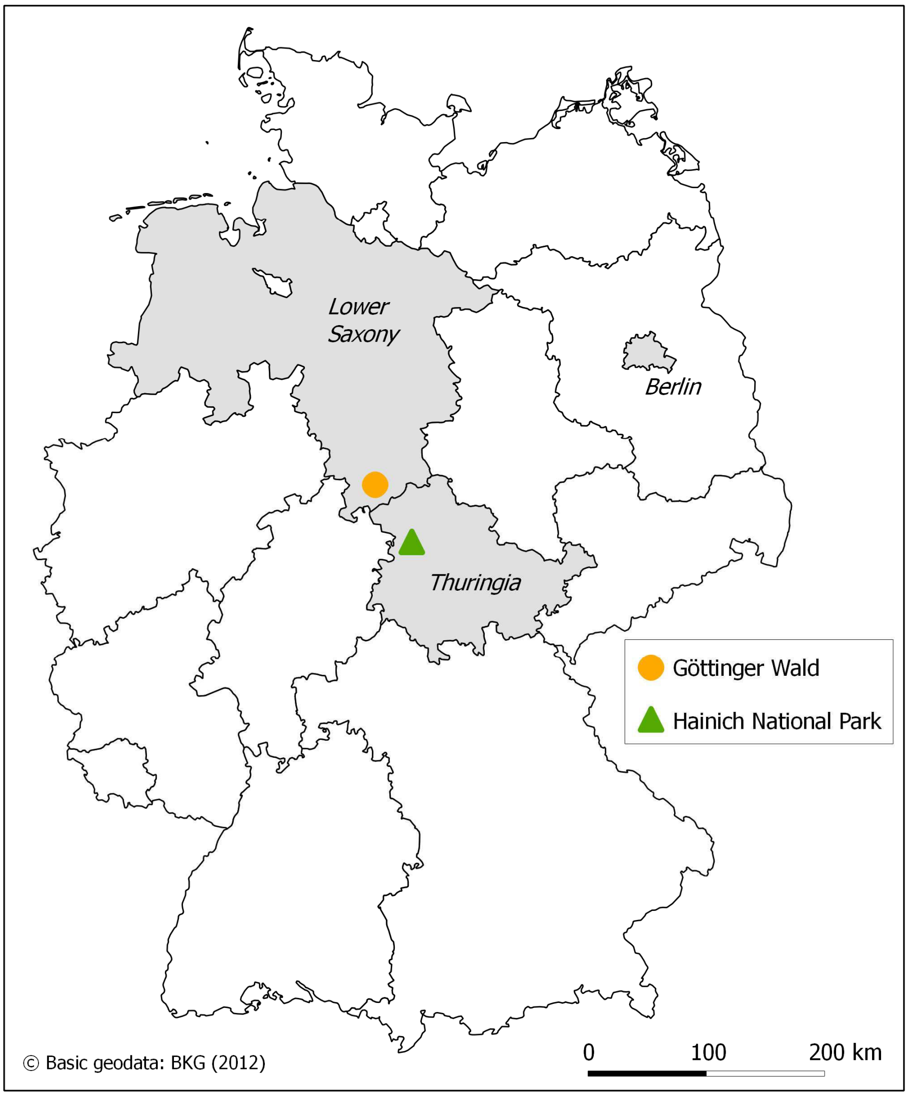

Fig. 1 Location of the study areas Hainich National Park and Göttinger Wald in the German federal states of Lower Saxony and Thuringia.

2.1.2 Study area Hainich National Park

In the Hainich study area, the 21 research sites are located on flat plateaus at about 350 m elevation in the north-eastern part of Hainich National Park (51°05’ N, 10°31’ E). The underlying bedrock is limestone from the Triassic Upper Muschelkalk formation. A closed, homogeneous loess-clay cover has developed as a result of loess deposition from the Pleistocene era. According to the World Reference Base for Soil Resources (WRB), the soil type of the research sites is (stagnic) Luvisol. The climate can be characterised as subatlantic with subcontinental influence; mean annual precipitation is ca. 590 mm with a mean annual temperature of ca. 7.5° C (Mölder et al., 2008, 2011). The middle of the 19th century saw an initial transition from the often irregular coppice with standards system (Mittelwald) to high forest (Hochwald), especially to the multiple aged stands with single-tree extraction (Plenterwald). The transition lasted until the early 20th century (Wäldchen et al. 2011). Since the study area became a military training area in 1964, only single stems have been extracted from the stands. In 1997, the Hainich National Park was founded and since then the study area is under strict nature protection (Mölder et al., 2006; Schmidt et al., 2009). Since 2012, the Hainich National Park is a component of the UNESCO World Heritage Site “Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany”. Dominant forest communities are the *Galio-Fagetum*, the *Hordelymo-Fagetum*, and the *Stellario-Carpinetum* (Mölder et al., 2006).

In addition to *Fagus sylvatica,* the major tree species in the 21 research sites are *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos*, *Acer pseudoplatanus*, *A. platanoides*, and *Carpinus betulus*. *Quercus petraea*, *Quercus robur*, and *Acer campestre* occur with no more than a few individuals in any of the research sites. The mean age of the Hainich stands varies between 80 and 190 years, and due to the former coppicing with standards and Plenterwald management a broad variety of age classes occurs, especially in the more diverse research sites (Schmidt et al., 2009).

2.1.3 Study area Göttinger Wald

In the Göttinger Wald study area (51°32’ N 09°56’ E), the 21 research sites are located on a plateau consisting of Lower Muschelkalk (Middle Trassic), elevation ranges from 380 to 420 m. The plateau is covered by a thin loess-clay layer. According to the World Reference Base for Soil Resources (WRB), the soil types of the research sites are Rendzic Leptosol and Calcaric Cambisol (Meesenburg et al., 2009; Schmidt and Streit, 2009). The climate can be

Tab. 1 Study areas Hainich National Park and Göttinger Wald: Floristic composition and forest species groups of vascular plants as well as overview of the diversity measures and environmental factors determined for all 42 research sites. MV = mean value, Min = minimum value, Max = maximum value. See Appendix Table A1 for a species list.

Study area		**Hainich**			**Göttinger Wald**		
Total area	**Floristic composition**						
	Total species richness		103			65	
	Forbs		64.1	%		61.5	%
	Graminoids		16.5	%		12.3	%
	Woody species		19.4	%		26.2	%
	Forest species groups						
	1.1 “Largely restricted to closed forest”		47.6	%		55.4	%
	1.2 "Prefers forest edges and clearings"		2.9	%		3.1	%
	2.1 “Occurs in forests as well as in open land”		46.6	%		41.5	%
	2.2 "May occur in forests, but prefers open land"		1.9	%		0	%
		Min	**MV**	**Max**	**Min**	**MV**	**Max**
21 Research sites ($400\ m^2$)	**Tree layer**						
	Species richness (SR)	1	3.9	7	1	2.3	4
	Shannon index (H')	0.00	0.83	1.65	0.00	0.56	1.25
	Fagus sylvatica proportion (%)	0	59	100	28	70	100
	Shrub layer						
	Cover (%)	0	1.9	8	3	31.8	80
	Species richness (SR)	0	1.0	3	2	4.4	7
	Herb layer						
	Species richness (SR)	10	30.8	53	13	22.7	31
	Shannon index (H')	1.15	2.45	3.34	1.31	2.13	2.77
	Biomass (g/m^2)	6.2	40.1	77.0	16.4	53.3	136.9
	Environmental parameters						
	Soil pH 0-10 cm (H_2O)	4.6	5.7	6.7	4.9	6.0	6.4
	Relative irradiance (%)	0.8	1.5	3.3	1.1	3.6	10.5
	Ellenberg indicator values						
	Light	3.6	4.3	4.7	3.1	3.7	4.1
	Reaction	5.6	6.5	6.8	5.9	6.5	6.9
	Nitrogen	5.1	5.9	6.6	4.8	5.3	5.6
	Moisture	4.9	5.4	5.8	5.1	5.2	5.4

characterised as subatlantic with low subcontinental influence. Mean annual precipitation amounts to ca. 709 mm and the mean annual temperature is ca. 7.4° C (Panferov et al., 2009). In the middle of the 19th century, a transition from the coppice with standards system to high forest started, which lasted until the early 20th century. Since the 1920s, close-to-nature forestry has been applied to the Göttinger Wald (Preutenborbeck, 2009). The dominant forest community is the *Hordelymo-Fagetum lathyretosum* (Schmidt, 2009). Aside from *Fagus sylvatica*, the main tree species are *Fraxinus excelsior* and *Acer pseudoplatanus* in the 21 research sites. *Acer platanoides*, *Carpinus betulus*, *Ulmus glabra*, and *Quercus robur* occur only sporadically. The mean age of the stands varies from 100 to 150 years and there have been no harvesting operations for at least three years prior to the investigation (Schmidt and Streit, 2009).

2.2 Hünstollen permanent plot study

In the vicinity of the 21 Göttinger Wald research sites, large parts of the strict forest nature reserve "Hünstollen" are located on similar sites on a plateau of 28 hectares (Schmidt, 2005; Fischer et al., 2009). The investigated stand has been unmanaged since 1989. It consists mainly of *Fagus sylvatica* with a mixture of *Acer pseudoplatanus* and *Fraxinus excelsior*. *Acer platanoides*, *Tilia platyphyllos*, and *Ulmus glabra* occur only sparsely. The Hünstollen reserve allows for a permanent plot investigation of tree- and herb-layer diversity changes over a 20-year period.

2.3 Sampling

2.3.1 Tree-layer diversity gradients

2.3.1.1 Tree layer

To characterise the stands with respect to tree-layer diversity at each research site, the relative canopy cover of all canopy-layer tree species (height > 500 cm) was visually estimated. For the purpose of characterising tree-layer diversity, the tree-layer species richness (tree-layer SR) and the Shannon index H' [$H' = -(p_i)(\ln p_i)$, where p_i = percentaged cover value of each species] were calculated (Magurran 2004). Furthermore, for each research site, the tree-layer *Fagus sylvatica* proportion of was determined based on relative canopy cover.

2.3.1.2 Herb layer

In each research site herb-layer species richness (herb-layer SR) and abundance were estimated by vegetation relevés. Due to the seasonal phenology of the herb-layer vegetation, sampling was conducted twice for each plot in 2005 (Hainich) and 2006 (Göttinger Wald) by estimating the percentage cover of each herb-layer species in spring and summer, respectively. For data analysis, spring and summer relevés were combined by taking the higher percentage cover value when a species was found in both relevés. To compare tree-layer diversity with herb-layer diversity, juvenile tree species were removed from the herb-layer data. In the course of the summer vegetation relevés the percentage cover of the shrub layer (height between 50 and 500 cm) was also estimated. For characterising herb-layer diversity, the herb-layer species richness (herb-layer SR) and the Shannon index H' [$H' = -(p_i)(\ln p_i)$, where p_i = percentaged cover value of each species] were calculated (Magurran, 2004). Nomenclature follows Wisskirchen and Haeupler (1998).

By using the model PhytoCalc (Bolte, 2006, Heinrichs et al. 2010), herbaceous biomass (g/m^2) as a proxy for actual herb-layer productivity (Axmanová et al., 2012) was calculated for each research site on the basis of vegetation relevés. This model calculates the herbaceous dry biomass from the percentage plant cover and average shoot lengths. PhytoCalc was calibrated with additional measurements of shoot lengths. Previous studies confirmed the calibration of PhytoCalc for both study areas from additional biomass harvests (Mölder et al., 2008; Schulze et al., 2009).

2.3.1.3 Abiotic environmental conditions

Since the upper 10 cm of soil are most significantly influenced by tree species effects (Augusto et al., 2002), we determined the soil pH (H_2O) of this soil layer by mixing four soil samples per 400 m^2 research site, each from 4-5 sampling points. Light conditions were estimated using PAR (photosynthetically active radiation) measurements made at 40 systematically distributed points on each plot. These measurements were conducted with LI-190 Quantum Sensors (Licor, Nebraska, USA) on overcast days with diffuse light conditions from July to August, 2005 (Hainich), and 2007 (Göttinger Wald), respectively. For each measurement, the relative irradiance RI was calculated as [RI = PAR stand / PAR nearest open area*100]. Mean values were computed for each research plot. Furthermore, mean Ellenberg indicator values for light, reaction, nitrogen and moisture (Ellenberg et al., 2001) were computed (qualitative evaluation) for each sample plot on the basis of the vegetation relevés (Diekmann, 2003).

2.3.2 Hünstollen permanent plot study

At 26 systematically distributed permanent plots (100 m x 100 m grid), vegetation relevés were conducted in an area of 250 m² in 1992 (Lambertz, 1993), 2002 (Ermert, 2003), and 2012 (by W. Schmidt). In all three sampling years, the percentage cover of each herb-layer species was estimated in both spring and summer (see 2.3.1.2. for more details). During the summer vegetation relevés, the percentage covers of the two tree layers (L2: height between 5 and 20 m, L1: height > 20 m) and the shrub layer (0.5-5 m) were also estimated.

2.4 Data analysis

2.4.1 Tree-layer diversity gradients

To investigate the interactions between tree layer, environmental factors, and herb layer, statistical analyses were conducted in two steps for the 21 research sites in each research area: firstly, an ordination to detect possible relationships between tree layer, environmental variables and herb-layer and secondly, a correlation analysis of the identified relationships (cf. Both et al., 2011; Durak 2012). To find those diversity and environmental variables significant for explaining differences in herb-layer species composition, multivariate analysis was applied to the vegetation data. To avoid an overestimation of common species, vegetation data was transformed using square root transformation. Vegetation data was then ordinated using an indirect ordination method: where species response was linear (length of gradient < 1.5; according to ter Braak and Prentice, 1988), a PCA (Principal Component Analysis; Goodall, 1954) was conducted; in the case of unimodal species responses (length of gradient > 1.5), a DCA (Detrended Correspondence Analysis; Hill and Gauch, 1980) was conducted.

A bi-plot was compiled by correlating diversity and environmental variables with the first two axes of the ordination diagrams. Those environmental variables found to be useful for explaining differences in herb-layer species composition were correlated (Spearman's rho [ρ]) with significant diversity variables, to determine whether herb-layer diversity is influenced by environmental variables affected by tree species diversity relationships (cf. Both et al., 2011; Durak 2012).

In order to compare floristic composition, species lists for each study area were prepared by pooling all species occurring in the 21 plots. To quantify the proportion of typical forest plant species, all species were assigned to one of the four forest species groups published by Schmidt et al. (2011):

- 1 Largely restricted to forest
    - 1.1 Largely restricted to closed forest
    - 1.2 Prefers forest edges and clearings
- 2 Occurrence in forest and open land
    - 2.1 Occurs in forests, as well as in open land
    - 2.2 May occur in forests, but prefers open land

We used the red list of the federal state of Lower Saxony (Garve, 2004) to identify threatened plants in the Göttinger Wald and the red list of the federal state of Thuringia (Korsch and Westhus, 2011) to identify threatened plants in the Hainich. In addition, we determined specially protected plants according to German federal law (BfN, 2013).

Indicator species analysis (Dufrene and Legendre, 1997) was performed to identify herb-layer species with an affinity to each of the two study areas. The indicator value of each species was tested for significance with a permutation test based on 9999 permutations.

For statistical analysis, we used the software PC-ORD (McCune and Mefford 2006) and R (version 2.15.2, R Development Core Team 2012) with the packages vegan and exactRankTests. Significance of statistic tests were noted as follows: *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$; n.s. = $p > 0.05$. SE = Standard error, SD = Standard deviation.

2.4.2 Hünstollen permanent plot study

With regard to the Hünstollen strict forest nature reserve in the Göttinger Wald, we prepared species lists for each sample year and assigned the plants to the four forest species groups according to Schmidt et al. (2011). We used the cumulative percentage covers ($\text{Cover}_{\text{L 1-3}}$) of the two tree layers (L 1 and L 2) and the shrub layer (L 3) as a proxy for light availability in the herb layer (Ewald et al., 2011; Axmanová et al., 2012). An appropriate formula to assess the cumulative percentage covers of multiple tree and shrub layers is given by Ewald et al. (2011). To avoid an overestimation of the cumulative cover, the overlap between the layers has to be substracted from their sum. As a property not directly observed in the field, the overlap is approximated as the product of cover proportions (J. Ewald, pers. comm.).

$$Cover_{L\,1-3} = \left(\left(\frac{L\,1}{100} + \frac{L\,2}{100} - \frac{L\,1}{100} * \frac{L\,2}{100}\right) + \frac{L\,3}{100} - \left(\frac{L\,1}{100} + \frac{L\,2}{100} - \frac{L\,1}{100} * \frac{L\,2}{100}\right) * \frac{L\,3}{100}\right) * 100$$

In the same way, the cumulative cover of *Fagus sylvatica* in the upper strata was calculated by applying the percentage cover values of *Fagus sylvatica* in each layer. Furthermore, mean Ellenberg indicator values for light (Ellenberg et al., 2001) were computed (qualitative evaluation) for each sample point on the basis of the vegetation relevés. Diversity and environmental variables were tested for differences between the three sampling years (Bonferroni-corrected Fisher Matched-Pairs Permutation Test; Welch and Gutierrez, 1988).

3. Results

3.1 Tree-layer diversity gradients

3.1.1 Study area Hainich National Park

The DCA (Fig. 2) clearly showed that understorey vegetation differed along a diversity gradient represented by the first axis regarding herb-layer species richness ($\rho = -0.86$) and *H'* ($\rho = -0.87$), as well as tree-layer species richness ($\rho = -0.62$) and *H'* ($\rho = -0.78$). The proportion of *Fagus sylvatica* in the tree-layer ($\rho = 0.78$) and herb-layer biomass ($\rho = -0.93$) were also correlated with the first axis. Additionally, the first axis showed an environmental gradient; it was negatively correlated with soil pH ($\rho = -0.77$), as well as Ellenberg indicator values for reaction ($\rho = -0.56$) and nitrogen ($\rho = -0.47$). Neither relative irradiance nor the Ellenberg indicator value for light was correlated with the axes 1 or 2.

Correlation analysis (Tab. 2) showed that tree-and herb-layer diversity measures were significantly positively correlated amongst themselves. Herb-layer diversity and soil pH were significantly negatively correlated with the *Fagus sylvatica* proportion in the tree-layer; the same is true for herb-layer biomass. Both tree- layer and herb-layer diversity were significantly positively correlated with soil pH. Furthermore, herb-layer biomass was significantly positively correlated with tree- and herb-layer diversity, soil pH, and Ellenberg indicator values for reaction and nitrogen.

3.1.2 Study area Göttinger Wald

The DCA (Fig. 3) showed that understorey vegetation differed along a diversity gradient represented by the second axis regarding herb-layer *H'* ($\rho = 0.76$) and herb-layer species richness ($\rho = 0.69$). The Ellenberg indicator values for reaction ($\rho = 0.68$) and light ($\rho = 0.56$), together with relative irradiance ($\rho = 0.42$) and soil pH ($\rho = 0.39$), were also positively correlated with the second axis. The *Fagus sylvatica* proportion in the tree-layer was only

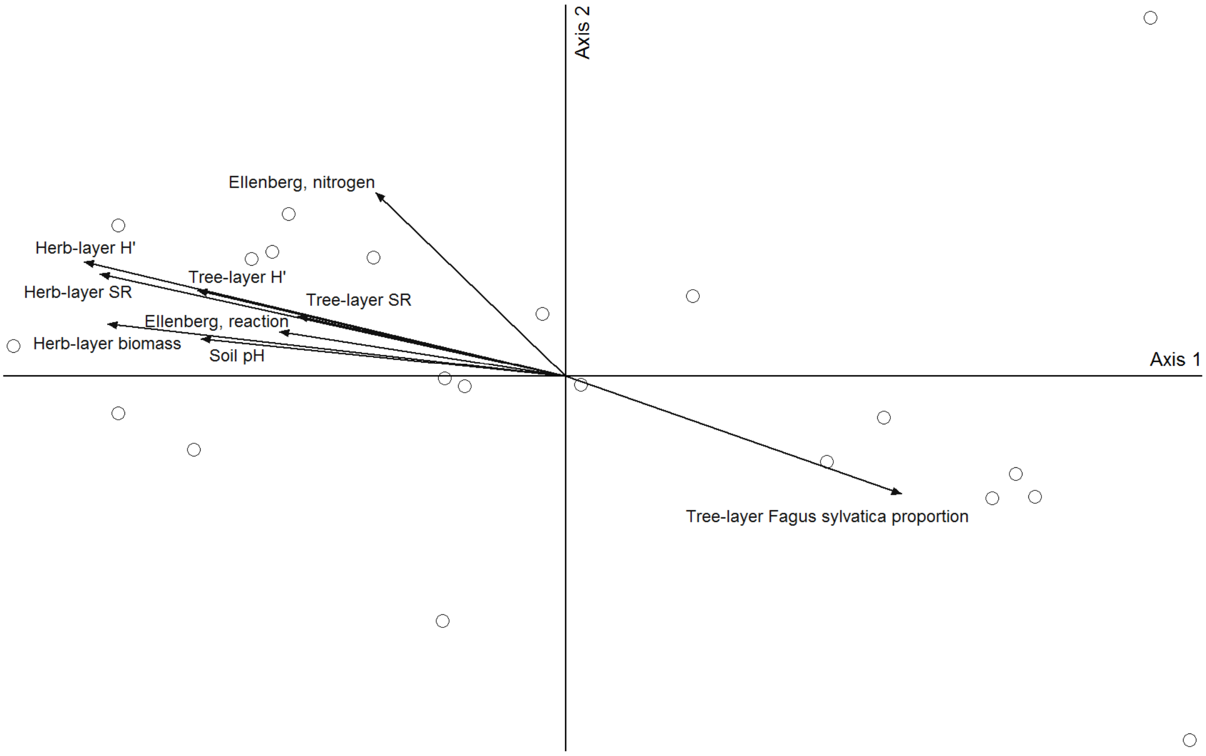

Fig. 2 Study area Hainich National Park: DCA of the herb-layer vegetation. A bi-plot was created by correlating diversity and environmental variables with axes 1 and 2. Matrix: 90 species, 21 relevés (axis 1: eigenvalue = 0.25, $R^2 = 0.79$, length of gradient = 2.20; axis 2: eigenvalue = 0.11, $R^2 = 0.03$). Correlation threshold: $R^2 > 0.25$.

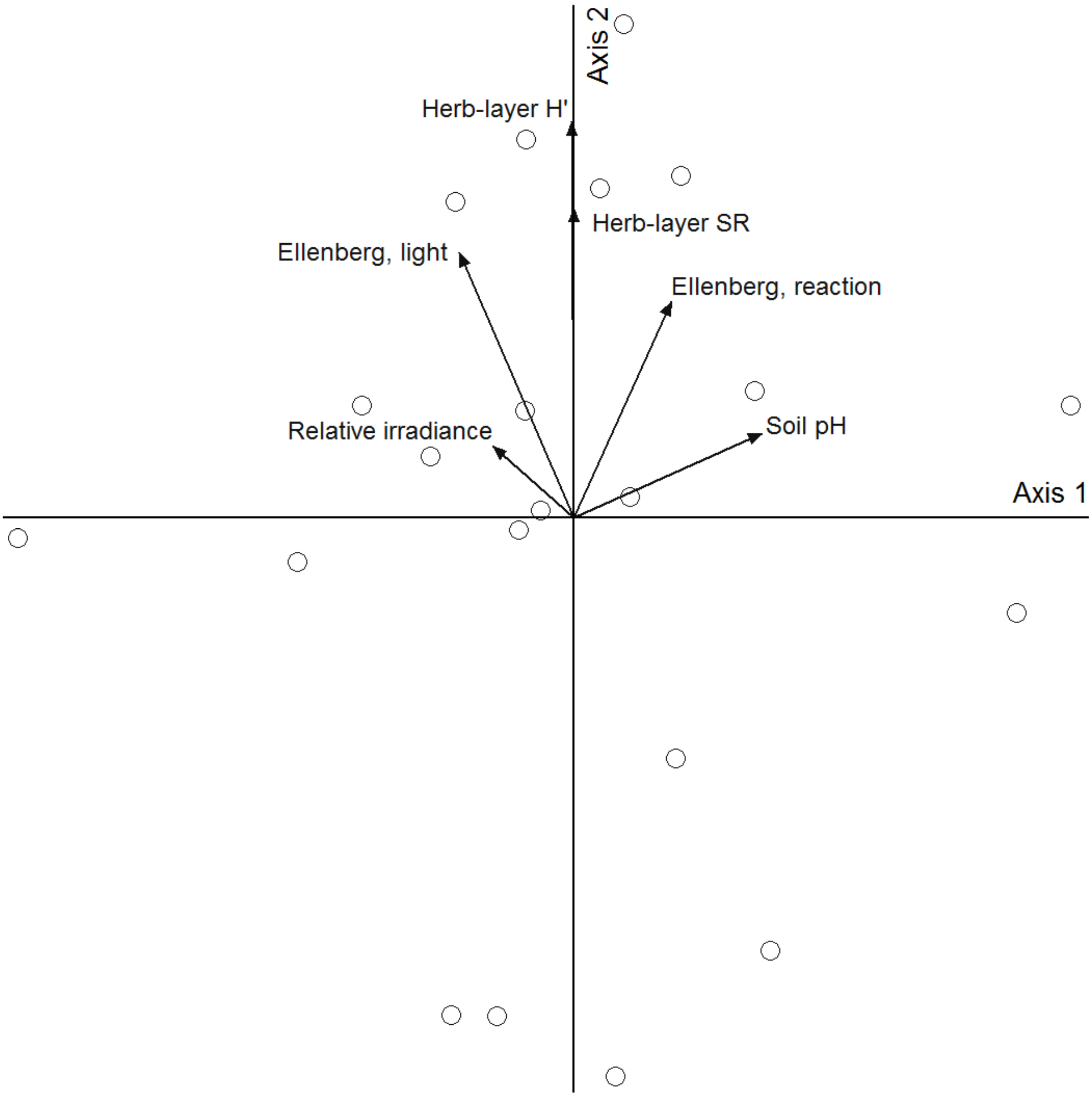

Fig. 3 Study area Göttinger Wald: DCA of the herb-layer vegetation. The bi-plot was created by correlating diversity and environmental variables with axes 1 and 2. Matrix: 53 species, 21 relevés (axis 1: eigenvalue = 0.17, $R^2 = 0.19$, length of gradient = 1.73; axis 2: eigenvalue = 0.09, $R^2 = 0.24$). Scaling: min. to max. Correlation threshold: $R^2 > 0.20$.

Tab. 2 Correlations between diversity and environmental variables in the study areas Hainich National Park and Göttinger Wald. N per study area = 21 research sites

HAINICH		**Herb layer**			**Measured variables**		**Ellenberg indicator values**	
		Species richness	**Shannon index *H′***	**Biomass (g/m²)**	**Soil pH 0-10 cm (H_2O)**	**Relative irradiance**	**Reaction**	**Nitrogen**
Tree layer		ρ	ρ	ρ	ρ	ρ	ρ	ρ
	Species richness (SR)	0.74 ***	0.70 ***	0.65 **	0.76 ***	-0.30 n.s.	0.34 n.s.	0.17 n.s.
	Shannon index (*H′*)	0.87 ***	0.85 ***	0.79 ***	0.85 ***	-0.28 n.s.	0.28 n.s.	0.20 n.s.
	Fagus sylvatica proportion (%)	-0.88 ***	-0.86 ***	-0.79 ***	-0.85 ***	0.24 n.s.	-0.29 n.s.	-0.18 n.s.
Herb layer								
	Species richness (SR)	-	-	0.87 ***	0.74 ***	-0.16 n.s.	0.39 n.s.	0.40 n.s.
	Shannon index (*H′*)	-	-	0.86 ***	0.73 ***	-0.12 n.s.	0.41 n.s.	0.45 *
	Biomass (g/m²)	-	-	-	0.74 ***	-0.34 n.s.	0.47 *	0.52 *

GÖTTINGER WALD		**Species richness**	**Shannon index *H′***	**Biomass (g/m²)**	**Soil pH 0-10 cm (H_2O)**	**Relative irradiance**	**Reaction**	**Light**
Herb layer				ρ	ρ	ρ	ρ	ρ
	Species richness (SR)	-	-	0.69 ***	0.12 n.s.	0.65 **	0.24 n.s.	0.73 ***
	Shannon index (*H′*)	-	-	0.60 **	0.17 n.s.	0.64 **	0.27 n.s.	0.73 ***
	Biomass (g/m²)	-	-	-	-0.18 n.s.	0.62 **	-0.19 n.s.	0.40 n.s.

marginally correlated with the first axis (ρ = -0.02) as well as the second axis (ρ = -0.003) and does not appear in Fig. 3.

Correlation analysis (Tab. 2) showed that relative irradiance was significantly positively correlated with herb-layer species richness and herb-layer *H'*, the same is true for the correlation between the Ellenberg indicator values for light and both herb-layer species richness and herb-layer *H'*. Furthermore, herb-layer biomass was significantly positively correlated with herb layer species richness, herb-layer *H'*, and relative irradiance.

3.1.3 Floristic composition and forest species groups for both study areas

Table 1 provides an overview of the floristic composition of both study areas; see Appendix Table A1 for a species list. With regard to forest species, the groups 1.1 "largely restricted to closed forest" and 2.1 "occurs in forests, as well as in open land" dominate in both study areas and include 95% of the species. With regard to specially protected plants (under German federal law), *Dactylorhiza maculata*, *Daphne mezereum*, *Epipactis helleborine*, *Leucojum vernum*, *Lilium martagon*, and *Orchis mascula* were found in the Hainich. In the Göttinger Wald, *Daphne mezereum* and *Hepatica nobilis* were noted. No threatened species, according to the red lists, were found.

The indicator values analysis showed that *Melica uniflora*, *Galium odoratum*, *Cardamine bulbifera*, and *Mercurialis perennis* were especially characteristic herb-layer species of the Göttinger Wald (Tab. 3). All of these species are assigned to the forest species group 1.1 "largely restricted to closed forest". With regard to the Hainich, particularly *Convallaria majalis, Ranunculus ficaria* subsp. *bulbilifer*, *Athyrium filix-femina*, and *Anemone nemorosa* can be considered as characteristic herb-layer species. These all belong to the forest species group 2.1 "occurs in forests, as well as in open land".

3.2 Hünstollen permanent plot study

In the Hünstollen strict forest nature reserve, the groups 1.1 "largely restricted to closed forest" and 2.1 "occurs in forests, as well as in open land" were dominant in all three sampling years and included 95% of the species (Tab. 4). The mean herb-layer species richness of the 26 sample points decreased from 31 to 21 between 1992 and 2012, with significant differences between the three sampling years. Also, the mean Ellenberg indicator value for light decreased, being significantly lower in 2012 than in 2002 and in 1992, even

Tab. 3 Study areas Hainich National Park and Göttinger Wald: Results of the indicator species analysis for the study areas Hainich and Göttinger Wald. Only species with p ≤ 0.001 are listed.

Species	Study area	Forest species group	Observed Indicator Value (IV)	IV from randomized groups		
				Mean	SD	p
Convallaria majalis	Hainich	2.1	81.0	29.5	7.53	0.0001 ***
Ranunculus ficaria subsp. *bulbilifer*	Hainich	2.1	81.0	27.9	6.26	0.0001 ***
Athyrium filix-femina	Hainich	2.1	71.4	25.5	6.33	0.0001 ***
Anemone nemorosa	Hainich	2.1	62.5	53.0	2.25	0.0003 ***
Dryopteris dilatata	Hainich	2.1	57.1	21.4	5.95	0.0002 ***
Lilium martagon	Hainich	2.1	57.1	20.8	5.47	0.0002 ***
Alliaria petiolata	Hainich	2.1	52.4	25.2	7.00	0.0004 ***
Ranunculus lanuginosus	Hainich	1.1	47.6	18.9	5.80	0.0004 ***
Lonicera periclymenum	Hainich	2.1	47.6	18.7	5.65	0.0005 ***
Melica uniflora	Göttinger Wald	1.1	99.9	36.2	7.17	0.0001 ***
Galium odoratum	Göttinger Wald	1.1	95.2	33.9	7.25	0.0001 ***
Cardamine bulbifera	Göttinger Wald	1.1	89.2	30.9	5.80	0.0001 ***
Mercurialis perennis	Göttinger Wald	1.1	84.9	41.3	8.12	0.0001 ***
Anemone ranunculoides	Göttinger Wald	1.1	83.9	48.2	5.11	0.0001 ***
Asarum europaeum	Göttinger Wald	1.1	80.8	42.0	6.85	0.0001 ***
Euphorbia amygdaloides	Göttinger Wald	1.1	76.2	26.0	5.74	0.0001 ***
Polygonatum verticillatum	Göttinger Wald	2.1	71.4	24.7	5.65	0.0001 ***
Oxalis acetosella	Göttinger Wald	1.1	64.1	26.2	5.91	0.0001 ***
Dryopteris carthusiana	Göttinger Wald	2.1	52.4	20.1	5.82	0.0002 ***

Tab. 4 Hünstollen permanent plot study: Total species richness and forest species groups in the three sampling years as well as overview of the diversity measures and environmental factors determined for all 26 sampling points. MV = mean value, Min = minimum value, Max = maximum value. Significant differences are indicated by different letters.

Sampling year		**1992**			**2002**			**2012**		
Total area	**Total species richness (incl. tree species)**		85			69			65	
	Forest species groups		**%**			**%**			**%**	
	1.1 “Largely restricted to closed forest”		51.8			52.2			60.0	
	1.2 "Prefers forest edges and clearings"		2.4			1.4			1.5	
	2.1 “Occurs in forests as well as in open land”		44.7			44.9			36.9	
	2.2 "May occur in forests, but prefers open land"		1.2			1.4			1.5	
26 Permanent plots (250 m^2)		**Min**	**MV**	**Max**	**Min**	**MV**	**Max**	**Min**	**MV**	**Max**
	Herb-layer species richness (excl. tree species)	21	30.7	41	15	27.7	34	6	20.8	29
			a			**b**			**c**	
	Standard error		1.0			1.0			1.0	
	Tree-layer species richness	1	1.9	3	2	2.2	4	1	2.1	3
			a			**a**			**a**	
	Standard error		0.1			0.2			0.1	
	Cumulative upper strata total cover (%)	63.3	86.0	100.0	76.8	93.4	103.0	81.2	92.0	100.0
			a			**b**			**b**	
	Standard error		1.8			1.2			1.0	
	Cumulative upper strata *Fagus sylvatica* cover (%)	33.5	69.3	91.5	65.9	81.8	94.4	40.2	79.3	93.0
			a			**b**			**b**	
	Standard error		3.2			1.6			2.3	
	Ellenberg indicator values for light	3.3	3.8	4.2	3.2	3.7	4.0	3.0	3.4	3.8
			a			**a**			**b**	
	Standard error		0.04			0.04			0.04	

though the decrease was moderate. With regard to the cumulative cover of the upper strata, we found an increase of about 7 % in the observation period, with a significant difference between 1992 and the two other sampling years (2002, 2012). The cumulative cover of *Fagus sylvatica* in the upper strata also increased. Between 2002 and 2012, a slight decline in the tree layer cover was recorded due to the storms “Kyrill” in 2007 and “Emma” in 2008.

4. Discussion

4.1 Relationships between tree-layer diversity and herb-layer diversity and productivity

Our study showed that herb-layer diversity is closely correlated to tree-layer diversity and beech abundance in Hainich National Park, while such a relationship could not be detected in the managed forest stands of the Göttinger Wald. These opposing results reflect the contradictory findings published in the literature, with studies comparing stands varying in composition and diversity of broadleaved tree species being quite rare (literature overview in Barbier et al., 2008; Mölder et al., 2008; Both et al., 2011; McEwan and Muller, 2011).
With regard to herb-layer productivity, the correlations to tree-layer diversity and beech abundance were on a par with those described for herb-layer diversity. Vockenhuber et al. (2011) also found that increasing tree-layer diversity was positively correlated with herb-layer cover (as a surrogate for herb-layer productivity) in Central German deciduous stands. Contrary to this, Both et al. (2011) concluded that herb-layer productivity is not affected by tree-layer diversity in Chinese subtropical broad-leaved forests.

However, what are the mechanisms responsible for the observed differences in the relationships between herb-layer diversity, herb-layer productivity, tree-layer diversity and tree-layer composition?

4.2 Herb-layer diversity as being ruled by canopy effects on soil properties and light regime

Canopy trees influence the herb layer stratum in different ways: either by their effect on the light availability for the herb layer as a result of the differing light transmissibility of the crowns, or their effect on soil structure and acidity through, for example, the litter decomposability (Augusto et al., 2003; Gilliam and Roberts, 2003; Neufeld and Young, 2003). These biological and chemical relationships between vegetation strata are regarded as responsible for diversity correlations by various authors (e.g., Barbier et al., 2008; McEwan and Muller, 2011; Bartels and Chen, 2013). Following Gilliam et al. (1995), such autogenic linkages between forest strata can be merely expected in mature stands - our investigated stands in the Hainich and in the Göttinger Wald agree with this.

In our study, chemical relationships between the forest strata appeared to be very influential for herb-layer diversity in the unmanaged Hainich stands. Here, we found that an increasing proportion of *Fagus sylvatica* in the tree layer was closely negatively correlated with herb-layer diversity and soil pH. We suppose that herbaceous understorey diversity was indirectly affected by the canopy tree species composition through the medium of the altered environmental factors soil pH and litter layer thickness (cf. Burton et al. 2011). The ecosystem changes, brought about by *Fagus sylvatica* ("ecosystem engineering") had, most likely, a major influence on these processes. Ecosystem engineers greatly modify environmental factors and thereby have an impact on the biocoenosis composition and ecosystem functioning (Jones et al., 1994). Various authors (e.g. Augusto et al., 2002; Aubert et al., 2004) conclude that *Fagus sylvatica* litter leads to more acidic soil conditions with a lower base saturation and nutrient supply. Additionally, beech foliage decomposes slowly, resulting in thick litter layers (Jacob et al., 2010). The rapidly decomposing litter of *Fraxinus excelsior*, *Carpinus betulus*, *Tilia* spp., *Ulmus glabra*, and *Prunus avium* results in more favourable soil conditions with a higher pH and base saturation (Augusto et al., 2002; Aubert et al., 2004; Langenbruch et al., 2012).

The resulting changes of ecological conditions on the forest floor along the tree diversity gradient, which are mainly caused by the increasing beech proportion in the canopy stratum, are supposed to affect the diversity of the herb-layer stratum. Particularly for species-rich beech forests, close negative correlations between decreasing soil pH and herb-layer diversity (Brunet et al., 1996; Härdtle et al., 2003; Borchsenius et al., 2004) as well as decreasing soil pH and seed bank diversity (Schmidt et al., 2009) were reported. Increasing litter layer thickness was also regarded as a factor that negatively affects herb-layer as well as seed bank density and diversity (Borchsenius et al., 2004; Barbier et al., 2008; Schmidt et al., 2009; Vockenhuber et al., 2011). Hence, we conclude that the increasing proportion of beech in the canopy stratum is responsible for the decreasing herb-layer diversity in the Hainich.

Contrary to the unmanaged Hainich stands, chemical relationships between the canopy- and the herb-layer stratum were not of importance in the managed Göttinger Wald stands, here the light factor was the crucial variable for herb-layer diversity. This basic difference can be explained by the differing light regimes (cf. Canham et al., 1990) in the two study areas. In the 21 Göttinger Wald research plots, we observed a pronounced gradient of relative irradiance from 10.5 % to 1.1 % (mean value = 3.6 %, SE = 0.6). The stands in the Hainich were considerably darker, relative irradiance ranged only between 3.3 % and 0.8 % (mean value = 1.5 %, SE = 0.1). This general darkness of the Hainich forest stands is the basic reason why particularly chemical variables become crucial for the development of herb-layer vegetation in this study area. Härdtle et al. (2003) found similar patterns in managed deciduous forests in Northern Germany: in dark beech forests the light factor had virtually no influence on herb-layer diversity (but base saturation had), while it was crucial for herb-layer diversity in lighter acidophytic beech and mixed beech–oak forests.

On the 21 Göttinger Wald research sites, where the light availability was the decisive variable for herb-layer diversity, the coverage of the shrub layer was much higher than in the Hainich due to silvicultural management and intensified roe deer hunting (Mölder et al., 2009b; Heinrichs et al., 2012). However, we found no significant relationship between shrub-layer cover and herb-layer diversity. Our results correspond to Bartels and Chen (2013), who emphasized that the shrub-layer stratum did not hinder the herb-layer stratum in Canadian boreal mixed-wood forests. This can be seen as an indication that tolerance or even facilitation between shrub- and herb-layer species may be a more important mechanism than competition between both strata (Chavez and Macdonald 2010b; Bartels and Chen, 2013).

4.3 Environmental and biological mechanisms determining herb-layer productivity

An effect of soil chemistry on herb-layer productivity was, as for herb-layer diversity, only observed in the Hainich study area and not in the Göttinger Wald. Generally, in both study areas, herb-layer productivity showed similar reactions and non-reactions to the light regime and to soil pH as herb-layer diversity did. In the Hainich, herb-layer productivity was positively correlated with soil pH and negatively with the proportion of *Fagus sylvatica* in the tree layer. This indicates that herb-layer productivity was promoted by an increased nutrient supply and base saturation in stands with high tree-species richness (Axmanová et al., 2012). In addition, an increasing beech proportion can be expected to interfere with herb-layer productivity, since beech has a dense fine root network in the topsoil and is a strong competitor for nutrients and water (Ellenberg and Leuschner, 2010). In the Göttinger Wald, herb-layer productivity increased with increasing light availability, which is an often reported phenomenon (Axmanová et al., 2012).

These findings are accompanied by a positive relationship between herb-layer productivity and diversity in both study areas, or were even stimulated by the diversity-productivity relationship. Such a positive relationship was also described by Axmanová et al. (2012) who observed positive species richness-productivity relationships in several deciduous forests throughout Europe. Outside of Europe, McEwans and Muller (2001) identified a unimodal relationship between diversity and productivity in the herb layer of an old-growth Appalachian forest. However, the intercorrelation between herb-layer diversity and productivity can hardly be separated from other biotic and environmental factors directly influencing productivity (Vilà et al., 2005).

4.4 Floristic composition and occurrence of forest plant species

In both the Hainich National Park and the Göttinger Wald (incl. the Hünstollen strict forest nature reserve), the flora was dominated by typical forest species (Schmidt et al., 2011). The absence of threatened species in both study areas can be related to the wide-ranging distribution of the occurring forest communities (Ellenberg and Leuschner, 2010). Several herb species which appeared to be characteristic for the Göttinger Wald (esp. *Asarum europaeum*, *Cardamine bulbifera*, and *Mercurialis perennis*) are typical plants of the forest community *Hordelymo-Fagetum* (wood barley beech forests) (Schmidt and Streit, 2009). For the Hainich, *Ranunculus ficaria* subsp. *bulbilifer* – a characteristic herb species of oak-hornbeam forests (*Stellarium-Carpinetum*) – was very typical. Oak-hornbeam forests are to a great extent the result of former silvicultural management in coppice with standards (Ellenberg and Leuschner, 2010). The constant occurrences of *Convallaria majalis* and other forest species assigned to the group 2.1 "occurs in forests, as well as in open land" might be relics from once brighter stand conditions of coppice with standard stands (Mölder et al., 2006, 2008; Schmidt et al., 2009, Altman et al., 2013). The slightly higher mean Ellenberg indicator value for light in the Hainich, as compared to the Göttinger Wald, can also be regarded as a relic from the once brighter stand conditions.

4.5 Effects of forest management on the tree- and herb-layer diversity patterns

As we have seen, the varying management practices or the lack of management in the two study areas resulted in different relationships between the canopy and the herb layer stratum. Most notably with regard to the light regime, recent forest management can largely explain the observed differences between the study areas. However, also century-old forest management decisions and practices still have a strong impact on the current diversity patterns:

The stands in the Hainich National Park area with their very high tree-species diversity are to a great extent the result of former silvicultural management of coppice with standards. Until the early 20th century, coppice with standards and oak-hornbeam forests were also common in the Göttinger Wald, but they vanished when the management system was changed to high forest (Preutenborbeck, 2009). As a result, the current tree-species richness is much higher in the Hainich than in the Göttinger Wald. The increased number of canopy species in the Hainich results in a more diverse site condition pattern (esp. soil pH) along the tree diversity gradient. Following the environmental heterogeneity hypothesis (Huston, 1994), these environmental differences result in a higher herb-layer diversity and overall species richness compared to the Göttinger Wald. This is also true when only considering the forest community *Hordelymo-Fagetum*: on average, the six *Hordelymo-Fagetum* research sites in the Hainich contain 4 canopy species (SE = 0.39) and 29 herbaceous species (SE = 2.18), while the 21 *Hordelymo-Fagetum* research sites in the Göttinger Wald contain 2 canopy species (SE = 0.25) and 23 herbaceous species (SE = 1.21). These results are contrary to Schmidt (2005) and Boch et al. (2013), who found that the richness of herbaceous forest species was generally lower in unmanaged forests compared to managed forests in German deciduous woodlands.

If we take the strict forest nature reserve Hünstollen in the Göttinger Wald as an example for strata interactions shortly after management cessation, we can see that the cover of the tree layer became significantly denser, which is a function of time since management cessation. As a consequence, both relative irradiance and herb-layer diversity decreased. Schmidt (2005) and Fischer et al. (2009) described similar processes from other strict forest nature reserves, where a decrease of herb-layer diversity was detected about 10 years after management cessation. With regard to forests growing on abandoned fields in New Hampshire, a comparable development was even observed for a longer period of time (Howard and Lee, 2003): during 200 years of forest development, the canopy stratum became increasingly denser and the diversity of the herb-layer stratum declined due to a decrease in available light. At the Hünstollen site, during the 20 years without felling operations, no tree diversity changes occurred in the canopy layer, since such processes need much more time (Gilliam et al, 1995; Fischer et al., 2009).

To predict the future long-term development of species-rich deciduous stands without management, we take the Hainich National Park as an example. Here, the former coppice with standard stand management system led to decreasing proportions of *Fagus sylvatica*, since this tree species has only a very low ability to resprout from the stump. When coppicing ceases, the competitive *Fagus sylvatica* regenerates from beechnuts and shows a high ability to spread out again (Mölder et al., 2009a; Ellenberg and Leuschner, 2010). Consequently, in the Hainich, species such as *Tilia* spp., *Fraxinus excelsior*, and *Carpinus betulus* with their meliorating litter can be expected, to a great extent, to be replaced by *Fagus sylvatica* in the future. Investigations of tree regeneration patterns in the Hainich support this conclusion (Huss and Butler Manning, 2006; Mölder et al., 2009b). As our results clearly show, an increasing proportion of *Fagus sylvatica*, which is accompanied by a decreasing proportion of the other broadleaved tree species, results in reduced herb-layer diversity. However, the secondary tree species cannot be expected to totally vanish in the Hainich. Sites with heavy clay soil promote *Tilia cordata,* but provide unfavourable growing conditions for *Fagus sylvatica* which does not thrive on temporary water-logged sites (Mölder et al., 2009a). Additionally, the frequency and intensity of storms, snow breaks and droughts will be decisive for the future tree species composition in the Hainich. After such large-scale disturbances, especially single specimens of *Fraxinus excelsior*, *Prunus avium, Acer pseudoplatanus*, and *Acer platanoides* have the chance to successfully compete with *Fagus sylvatica* – but such chances are quite infrequent and depend particularly on the population density of browsing deer (Huss and Butler Manning, 2006; Kompa and Schmidt, 2006; Mölder et al., 2009b; Heinrichs and Schmidt 2013). Since the large herbivores wisent, aurochs and wild horse have almost totally vanished from Europe, these animals can be excluded as a factor that opposes the dominance of beech and might be able to support the growth of other tree species by creating a more open forest structure (Birks, 2005). With regard to *Fraxinus excelsior*, the further development of the currently raging ash dieback will also play a decisive role (Pautasso et al., 2013).

5. Conclusions

We found that the cessation of forest management for conservational reasons might result in a decreasing herbaceous forest species diversity and productivity in many European deciduous woodlands. This is especially true for landscapes where former management practices, such as coppicing with standards, led to high tree-species richness and a reduced abundance of *Fagus sylvatica*. The short-term consequences of management cessation are losses in herb-layer diversity due to reduced light availability. In the long run, herb-layer diversity and productivity will decrease due to the expansion of the competitive ecosystem engineer *Fagus sylvatica*. If the conservational intention is to preserve and develop the typical diversity of near-natural beech forests, completely ceasing forest management can be advised. In this case, tree- and herb-layer diversity will decrease, while the diversity of other organisms, for example, saproxylic beetles, mushrooms or lichens, might increase (Paillet et al., 2010). However, if the typical forest herb diversity of the semi-natural, century-old cultural landscape is to be conserved, close-to-nature forestry management is necessary (Peterken, 1996). This also implies reactivating forest management systems such as coppicing or coppice with standards (Geb et al., 2004; Albert and Ammer, 2012).

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6. Literature

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Appendix Table A1 Species list of the study areas Hainich National Park and Göttinger Wald.

Life form groups: f = forb; g = graminoid; w = woody species

Forest species groups:

1 Largely restricted to forest
  1.1 Largely restricted to closed forest
  1.2 Prefers forest edges and clearings
2 Occurrence in forest and open land
  2.1 Occurs in forests as well as in open land
  2.2 May occur in forests, but prefers open land

			Study area		
No.	**Species**	**Life form group**	**Hainich**	**Göttinger Wald**	**Forest species group**
1	*Actaea spicata*	f	x		K1.1
2	*Aegopodium podagraria*	f	x		K2.1
3	*Alliaria petiolata*	f	x		K2.1
4	*Arctium nemorosum*	f	x		K1.2
5	*Athyrium filix-femina*	f	x		K2.1
6	*Bromus ramosus*	g	x		K1.1
7	*Calamagrostis arundinacea*	g	x		K2.1
8	*Cardamine pratensis*	f	x		K2.1
9	*Carex digitata*	g	x		K1.1
10	*Carex muricata* agg.	g	x		K2.1
11	*Chaerophyllum temulum*	f	x		K1.2
12	*Convallaria majalis*	f	x		K2.1
13	*Dactylorhiza maculata*	f	x		K2.1
14	*Dryopteris dilatata*	f	x		K2.1
15	*Epipactis helleborine*	f	x		K1.1
16	*Euonymus europaea*	f	x		S2.1
17	*Festuca altissima*	g	x		K1.1
18	*Festuca gigantea*	g	x		K1.1
19	*Festuca heterophylla*	g	x		K1.1
20	*Gagea lutea*	f	x		K1.1
21	*Galium aparine*	f	x		K2.1
22	*Geranium dissectum*	f	x		-
23	*Gymnocarpium dryopteris*	f	x		K1.1
24	*Hieracium murorum*	f	x		K2.1
25	*Hypericum perforatum*	f	x		K2.2
26	*Lathraea squamaria*	f	x		K1.1
27	*Leucojum vernum*	f	x		K2.1
28	*Lilium martagon*	f	x		K2.1
29	*Listera ovata*	f	x		K2.1
30	*Lonicera periclymenum*	w	x		S2.1
31	*Luzula multiflora*	g	x		K2.1
32	*Maianthemum bifolium*	f	x		K1.1
33	*Moehringia trinervia*	f	x		K1.1
34	*Mycelis muralis*	f	x		K2.1
35	*Orchis mascula*	f	x		K2.1
36	*Paris quadrifolia*	f	x		K1.1
37	*Phyteuma spicatum*	f	x		K2.1
38	*Poa nemoralis*	g	x		K2.1
39	*Poa trivialis*	g	x		K2.1
40	*Ranunculus ficaria* subsp. *bulbilifer*	f	x		K2.1
41	*Ranunculus lanuginosus*	f	x		K1.1
42	*Rubus fruticosus* agg.	w	x		S2.1
43	*Rumex conglomeratus*	f	x		K2.2
44	*Sambucus nigra*	w	x		S2.1
45	*Sanicula europaea*	f	x		K1.1
102	*Quercus petraea*	w	x		B2.1
103	*Tilia cordata*	w	x		B1.1
46	*Ajuga reptans*	f	x	x	K2.1
47	*Allium ursinum*	f	x	x	K1.1
48	*Anemone nemorosa*	f	x	x	K2.1

49	*Anemone ranunculoides*	f	x	x	K1.1
50	*Arum maculatum*	f	x	x	K1.1
51	*Asarum europaeum*	f	x	x	K1.1
52	*Brachypodium sylvaticum*	g	x	x	K1.1
53	*Campanula trachelium*	f	x	x	K1.1
54	*Cardamine bulbifera*	f	x	x	K1.1
55	*Carex sylvatica*	g	x	x	K1.1
56	*Circaea lutetiana*	f	x	x	K1.1
57	*Corydalis cava*	f	x	x	K1.1
58	*Crataegus laevigata*	w	x	x	S2.1
59	*Dactylis polygama*	g	x	x	K1.1
60	*Daphne mezereum*	w	x	x	S1.1
61	*Deschampsia cespitosa*	g	x	x	K2.1
62	*Dryopteris filix-mas*	f	x	x	K1.1
63	*Fragaria vesca*	f	x	x	K2.1
64	*Galium odoratum*	f	x	x	K1.1
65	*Galium sylvaticum*	f	x	x	K1.1
66	*Geranium robertianum*	f	x	x	K2.1
67	*Geum urbanum*	f	x	x	K2.1
68	*Hedera helix*	w	x	x	S1.1
69	*Hordelymus europaeus*	g	x	x	K1.1
70	*Impatiens parviflora*	f	x	x	K1.1
71	*Lamium galeobdolon*	f	x	x	K1.1
72	*Lapsana communis*	f	x	x	K2.1
73	*Lathyrus vernus*	f	x	x	K1.1
74	*Melica uniflora*	g	x	x	K1.1
75	*Mercurialis perennis*	f	x	x	K1.1
76	*Milium effusum*	g	x	x	K1.1
77	*Oxalis acetosella*	f	x	x	K1.1
78	*Polygonatum multiflorum*	f	x	x	K1.1
79	*Primula elatior*	f	x	x	K2.1
80	*Pulmonaria officinalis*	f	x	x	K1.1
81	*Ranunculus auricomus* agg.	f	x	x	K2.1
82	*Rubus idaeus*	w	x	x	S2.1
83	*Scrophularia nodosa*	f	x	x	K2.1
84	*Senecio ovatus*	f	x	x	K1.2
85	*Sorbus aucuparia* subsp. *aucuparia*	w	x	x	B2.1
86	*Stachys sylvatica*	f	x	x	K1.1
87	*Stellaria holostea*	f	x	x	K1.1
88	*Taraxacum* sect. *Ruderalia*	f	x	x	K2.1
89	*Urtica dioica*	f	x	x	K2.1
90	*Vicia sepium*	f	x	x	K2.1
91	*Viola reichenbachiana*	f	x	x	K1.1
92	*Acer campestre*	w	x	x	B2.1
93	*Acer platanoides*	w	x	x	B2.1
94	*Acer pseudoplatanus*	w	x	x	B2.1
95	*Carpinus betulus*	w	x	x	B1.1
96	*Fagus sylvatica*	w	x	x	B1.1
97	*Fraxinus excelsior*	w	x	x	B2.1
98	*Prunus avium*	w	x	x	B2.1
99	*Quercus robur*	w	x	x	B2.1
100	*Tilia platyphyllos*	w	x	x	B1.1
101	*Ulmus glabra*	w	x	x	B1.1
104	*Crataegus monogyna*	w		x	S2.1
105	*Dryopteris carthusiana*	f		x	K2.1
106	*Euphorbia amygdaloides*	f		x	K1.1
107	*Glechoma hederacea*	f		x	K2.1
108	*Hepatica nobilis*	f		x	K1.1
109	*Hypericum hirsutum*	f		x	K1.2
110	*Juncus effusus*	g		x	K2.1
111	*Polygonatum verticillatum*	f		x	K2.1
112	*Lonicera xylosteum*	w		x	S1.1
	Sum		103	65	