Effects of forest management intensity on herb layer plant diversity and composition of deciduous forest communities in Northern Germany

Effekte der Waldbewirtschaftungsintensität auf die Diversität und Artenzusammensetzung der Krautschicht von Laubwaldgesellschaften in Norddeutschland

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Abstract

Forest management is assumed to significantly affect herb layer species richness and community composition. Thus, the main objective of this study was to assess the effects of a reduction in forest management intensity on herb layer species assemblages in deciduous forests of Northern Germany. We selected forest stands which had been managed according to different management intensities (i.e., single-tree and group selection harvest) up to the year 1994, and which were subject to a low-impact management approach (i.e., single-tree harvest with minimal thinning interventions and the development of high growing stocks) since then. Unmanaged forest stands were used as a reference for the managed stands. Results from a previous study using vegetation data recorded in 1997 showed that species richness and compositional differences of the herb layer increased significantly with management intensity. The present study is based on a re-survey of these forest stands after 17 years. We therefore hypothesized that – as a result of the less intensive the forest management – the herb layer in both types of managed stands became more similar to that of the unmanaged stands over time. Specifically, we expected the changes in the stands with former group selection harvest to be stronger than those of the stands with former single-tree selection harvest. We found that herb layer species richness and cover decreased considerably over time, and that these changes were most pronounced in stands with the formerly more intensive management (i.e., former group selection harvest). Detailed analyses of species composition and species groups of the herb layer revealed that only a few differences remained in the managed stands when compared to the unmanaged stands. These differences are suggested to be related to previous soil disturbances in synergy with canopy openings. Our results suggest that a minimal intervention single-tree selection harvest system may have a low impact on the typical forest herb layer communities, and that a shift to low-intensity management may lead to a recovery of the plant communities over time even in formerly more intensively managed stands.

Keywords: biodiversity change, deciduous forests, forest management intensity, understorey vegetation, vegetation resurvey

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Facing the conflicting demands of higher timber production and protection of forest biodiversity (BMU 2007, BERGSENG et al. 2012), integrative approaches to cover both sustainable forestry and nature conservation in European forests came into focus in recent years (KRUMM et al. 2013). In this context, naturalness and protection of natural processes have become guiding principles of modern forest management in Europe (STURM 1993, KRUMM et al. 2013). Both require a deeper understanding of the ecosystem dynamics of forests and a continuous observation of potential management impacts on forest biodiversity and processes (FISCHER 2011). As remnants of primary forests in Central Europe are scarce, strict forest reserves can serve as a proxy for natural forest dynamics, and thus the degree of naturalness (e.g., naturalness of site conditions, vegetation composition and development; WESTPHAL et al. 2004, PARVIAINEN 2005, KRUMM et al. 2013).

Forest management affects forest ecosystems in space and time by altering tree species composition, age class distribution, life cycle duration and structural attributes such as vertical stratification, tree density and biomass stocks. It thereby influences light availability, temperature, moisture, water balance, litter layer, top-soil conditions and the spectrum of habitats (GRAAE & HESKJÆR 1997, MA et al. 2010, SCHMIDT 2013). Nature-oriented forest management aims to mimic natural stand dynamics and structures in managed forests and pursues a reduction of management-related impacts on forest ecosystems. However, forest management strategies greatly vary with respect to thinning or harvest frequency and intensity, which results in differences in light (e.g., canopy gap sizes) and soil conditions (e.g., water and nutrient supply) (DECOQC et al. 2004, KUULUVAINEN 2009, VON OHEIMB & HÄRDTLE 2009).

For assessing the impact of forest management, the herb layer communities often function as an indicator for the present conditions and the integrity of a forest ecosystem (SCHMIDT 2005, BOCH et al. 2013). Understorey communities have shown to respond rapidly to environmental changes in abundance patterns and species composition, however, this response can be much slower in closed-canopy forests (SCHMIDT 2005, FISCHER et al. 2009, BERNHARDT-RÖMERMANN et al. 2015, DE FRENNE et al. 2015). Several studies aimed at identifying herb layer patterns in response to nature-oriented management and environmental conditions by comparing managed and unmanaged stands (DECOQC et al. 2004, MEYER & SCHMIDT 2008, VON OHEIMB & HÄRDTLE 2009, PAILLET et al. 2010, FISCHER 2011, EWALD & ENDRESS 2015), by following vegetation dynamics after cessation of management in strict forest reserves (HUSS & BUTLER-MANNING 2006, FISCHER et al. 2009, HEINRICHS et al. 2012, 2014; SCHMIDT & HEINRICHS 2012, SCHMIDT 2013) or, less frequently, by analysing natural dynamics in old-growth forest relicts (VON OHEIMB et al. 2004, DITTRICH et al. 2013). However, research has, so far, not addressed responses of herb layer vegetation towards a reduction of forest management intensity by using minimal intervention harvest systems analysing long-term empirical data with a chronosequence approach.

Beech-dominated forests represent the natural vegetation in large parts of Central Europe (BOHN 2003, ELLENBERG & LEUSCHNER 2010). After millennia of management, deforestation and forest fragmentation, beech forests have been strongly reduced in the areal extent, and the remaining stands are mostly managed. While forest management have been shown to increase the diversity of vascular plants, primeval and protected beech forests commonly exhibit a small-scale natural disturbance regime that may lead to a relatively species-poor community of vascular plants (KORPEL 1995, VON OHEIMB & HÄRDTLE 2009, SCHIEBER & JANÍK 2012). Therefore, it is argued that management-related disturbances in forests would

enhance vascular plant species diversity due to larger (micro-)habitat heterogeneity (e.g., due to logging trails, soil disturbance and compaction, clearings; VON OHEIMB & HÄRDTLE 2009, MÖLDER et al. 2014).

The present study aims to explore the long-term effects of a reduction of forest management intensity on herb layer diversity and composition of lowland deciduous forest communities in Northern Germany. For detecting responses of herb layer communities on forest management intensity, two major approaches of vegetation analysis are being combined: (a) a chronosequential comparison of the herb layer vegetation in managed and unmanaged stands using a space-for-time approach (JOHNSON & MIYANISHI 2007), and (b) a time sequence in terms of a re-survey of the vegetation relevés conducted by VON OHEIMB (2003) in 1997. In the study of VON OHEIMB (2003) the investigated stands depicted a management intensity gradient from unmanaged reference stands over low-intensity single-tree selection harvest to moderate intensity, group selection harvest. From the year 1994 on, the managed stands were uniformly treated in a minimal intervention single-tree selection harvest system (STADTWALD LÜBECK 2004, FICHTNER et al. 2012). Conducting a re-survey of the vegetation in the year 2014, we wanted to test the hypotheses that (1) the herb layer in both types of managed stands became more similar to that of the unmanaged stands over time, and (2) that the changes in the stands with former group selection harvest were stronger than those of the stands with former single-tree selection harvest.

2. Material and Methods

2.1 Study area and selection of forest stands

This study includes eight forest stands located in the municipal forest of Lübeck in south-eastern Schleswig-Holstein and Mecklenburg-Western Pomerania at a mean altitude of 20–90 m a.s.l. (North Germany, 53°35'–53°47' N, 10°30'–10°47' E). The study area is characterized by a suboceanic climate (annual precipitation sum between 580 and 871 mm; mean annual temperature 8.3 °C; GAUER & ALDINGER 2005). The dominant geological substrate is boulder clay with associated soils like luvisols, gleyic luvisols and stagnic gleysols, the dominant humus type is mull (VON OHEIMB 2003, VON OHEIMB & HÄRDTLE 2009). Forest vegetation of the study area is naturally dominated by deciduous forests, particularly Woodruff-beech forests (*Galio odorati-Fagetum* Sougnez et Thill 1959) and oak-hornbeam forests (*Stellario-Carpinetum* Oberd. 1957). While *Fagus sylvatica* dominates the tree layer of the investigated stands, all stands include certain admixtures of broadleaved tree species such as *Carpinus betulus*, *Acer pseudoplatanus*, *Quercus robur* and *Fraxinus excelsior* (Supplement E1). All stands are uneven-aged high forests with mean stand ages of 120 up to 210 years.

Up to 1994, silvicultural interventions involved thinning treatments, salvage harvest and target diameter harvest (VON OHEIMB & HÄRDTLE 2009). In case of the latter, trees were removed when they reached a target diameter at breast height (DBH) of 60 cm (*F. sylvatica*, *F. excelsior*, *A. pseudoplatanus*) and 80 cm (*Q. robur*, *Q. petraea*), respectively. Single-tree selection canopy openings were typically smaller than 0.02 ha, while group selection canopy openings ranged from 0.04 to 0.3 ha. As a consequence, the managed forest stands differed with regard to the canopy gap size created by the harvest interventions. Supplement E1 provides an overview on harvest intensity (expressed as the amount of timber volume harvested per stand) and the frequency of silvicultural interventions in the periods from 1980 to 1997 and from 1998 to 2013.

Since 1994, managed stands are subjected to a nature-oriented management approach, being certified according to the labels of 'Naturland' (1997) and FSC (1998) (STADTWALD LÜBECK 2004, FICHTNER et al. 2012, 2013). This approach aims at (i) approximating natural dynamics, structures and species compositions in the managed forests, (ii) setting and accomplishing appropriate economic targets that do not overcharge ecosystem capability and resilience, and (iii) following the principle of

minimal intervention. Furthermore, at least 10% of the total forest area of the municipal forest of Lübeck remains unmanaged and serves as local "reference areas" for understanding the natural forest dynamics. In beech and oak forests forest management includes exclusively single-tree selection harvest based on the target DBH of trees (75 cm for *F. sylvatica* and 80 cm for *Q. robur*, *Q. petraea*) and no thinning interventions above a DBH of 30 cm (STADTWALD LÜBECK 2004, STURM 2013). Over two decades, therefore, the managed stands selected for this study were subjected to a uniform minimal intervention system. All unmanaged stands were located in the Schattin forest (50 ha in size), where forest management interventions ceased in 1950 due to its location near the former border between the German Democratic Republic and the Federal Republic of Germany (VON OHEIMB 2003). In 1994, this forest became part of the unmanaged reference areas.

2.2 Vegetation sampling

Based on the vegetation relevés of VON OHEIMB (2003, year of record: 1997), we performed a re-survey in 2014 (Supplements E2 and E3). The analyses are based on 85 sample plots in 1997, and 49 sample plots in 2013, which are distributed over eight forest stands (Supplement E1). As the sample plots from 1997 had not been permanently marked in the field, relevés were re-sampled as semi-permanent plots (VON OHEIMB & BRUNET 2007, HEINRICHS et al. 2012). In 2014, plots were set up at the intersection points of a permanent forest inventory grid of the forestry office of the city of Lübeck in order to prevent a surveyor-biased selection. Sites close to the forest edge and sites with locally higher soil moisture (drainage ditches, stream embankments) were excluded. Replicating the survey method of VON OHEIMB (2003), vegetation was recorded in 200 m^2 squares during July and August 2014, with restriction on vascular plants. Species cover was estimated separately for the herb (< 1 m), shrub (> 1 m – 5 m), and tree layer (> 5 m). Saplings of woody species < 1 m in height were considered as herb layer species. The cover of the relevant species was estimated using 5% intervals. Below 10% species cover, the scale was refined (0.1, 0.5, 1, 2, 3, 5 and 8%). Plant nomenclature follows BUTTLER & HAND (2008).

In order to estimate light availability below tree and shrub canopy and to assess canopy cover heterogeneities as consequences of gap creation, the leaf area index (LAI) and the standard error of the LAI (SEL) were measured using a LAI-2200 Plant Canopy Analyzer (LI-Cor, Lincoln, U.S.). Measurements were performed at cloudy conditions, before sunrise or after sunset at a height of 1 m above ground between July 28th and July 30th 2014.

2.3 Data analyses

Based on harvest severity in the period from 1980 to 1997, VON OHEIMB (2003) assigned all stands to three management intensity types: unmanaged (UM), single-tree selection (M1) and group-selection (M2) management. In the present study these groups were kept, all the managed stands, however, underlie a minimal intervention single-tree selection harvest system since 1994 (see above). Analyses of plant diversity were based on species richness (α-diversity) and total herb layer cover. Species richness was calculated as the total species number per relevé. Total cover was calculated by summing up the cover percentages of all individual species per relevé.

In order to assess the impact of forest management on herb layer composition and abundance patterns, two classifications were made. Based on the classification of SCHMIDT et al. (2011) for the North German lowland, herb layer species were grouped as strict forest species (1.1), species of forest edges and clearings (1.2), indifferent species (2.1), and indifferent species more common in open land habitats (2.2). Secondly, herbs were classified as disturbance indicators (DI), referring to the DI definition for mesic, beech-dominated forests (GRABHERR et al. 1998). Unweighted Ellenberg indicator values (for light, soil moisture, reaction and nitrogen) were calculated for each plot as a proxy for environmental conditions (DIERSCHKE 1994, ELLENBERG et al. 2001).

As the vegetation relevés of 1997 could not be precisely relocated (see above), the plots could not be compared pairwise. Therefore, plot level data of both sample years, 1997 and 2014, were averaged for each stand and the comparisons were conducted at stand-level (HÉDL 2004).

Differences in species richness, cover, Ellenberg indicator values, LAI and SEL between the three management intensity types (UM, M1, M2) were tested by one way ANOVA, followed by a post-hoc test (Tukey HSD). Relationships between species richness and cover data for the total herb layer and species groups and management intensity, tree layer cover, LAI, SEL and Ellenberg indicator values were tested by Pearson's product moment correlation. Moreover, we performed an indicator species analysis ('indic.species') to explore differences in species assemblages among management intensity types. This analysis assesses the strength and the statistical significance of the relationship between species occurrence/abundance and groups of sites (here: the management intensity type) as well as tests the statistical significance of these associations (DE CACERES & JANSEN 2016). All analysis were performed for each sampling year separately.

For data analyses, we used the software R version 3.0.2 (R CORE TEAM 2013), particularly the R package 'indic.species' for identifying indicator species.

3. Results

3.1 Tree and shrub layer

Significant differences in the tree layer cover were observed between the unmanaged and managed stands in 2014 (Fig. 1). The unmanaged stands had a significantly higher cover than the managed stands, and showed also the highest homogeneity in the tree layer. In the shrub layer, low coverages were observed across all unmanaged stands, whereas cover values of the managed stands varied from 4% to 37% (Fig. 1). Shrub cover was significantly higher in the stands with former group selection harvest than in the unmanaged and formerly single-tree selection harvested stands.
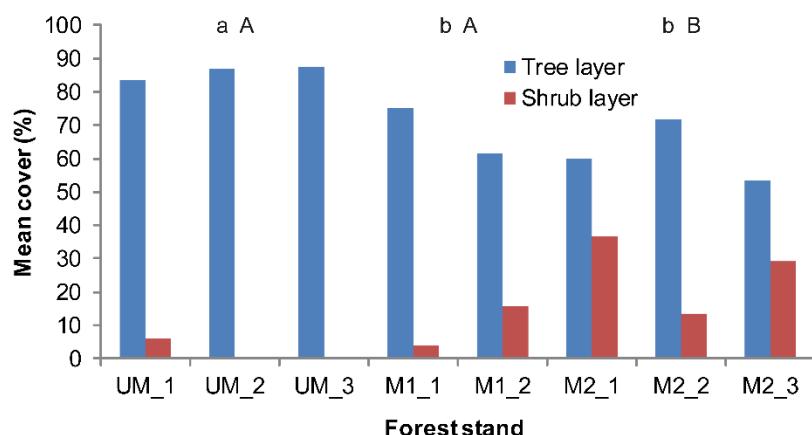
Fig. 1. Mean cover (%) of the tree and shrub layer in 2014 in stands of the three management intensity types: UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection harvest; M2, group selection harvest. Numbers after the underscore denote the specific stand (see Supplement E1). Different lower-case letters (tree layer) and upper-case letters (shrub layer) indicate significant differences among management types (one way ANOVA with post-hoc Tukey's test; $p < 0.05$).

Abb. 1. Mittlere Deckungsgrade (%) der Baumschicht und der Strauchschicht in 2014 in Beständen der drei verschiedenen Bewirtschaftungsintensitätstypen: UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme. Zahlen nach dem Unterstrich bezeichnen den einzelnen Bestand (s. Anhang E1). Verschiedene Kleinbuchstaben (Baumschicht) bzw. Großbuchstaben (Strauchschicht) bezeichnen signifikante Unterschiede zwischen den Bewirtschaftungsintensitätstypen (one-way ANOVA mit post-hoc Tukeys Test; $p < 0,05$).

3.2 Herb layer species richness and cover

Overall, a strong decline in species richness and total cover of the herb layer was found between 1997 and 2014, being larger in managed than in unmanaged stands (Table 1, Figs. 2 and 3). In 1997, significant differences in total species richness and total herb layer cover were found between all management types, whereas these differences were not significant in 2014. The same pattern was found for the number of strict forest species (group 1.1) and of species of forest edges and clearings (group 1.2). The cover values of these groups, however, did not differ between the unmanaged stands and the single-tree selection harvest stands in 1997, whereas they were significantly higher in the group selection stands. Species richness and cover of these two species groups did not differ in 2014.

The mean number of indifferent species (group 2.1) showed a slight tendency of increase with increasing management intensity in both sampling years. These differences were, however, not statistically significant (Table 1). Whereas in 1997 the cover of this group was significantly higher in the managed stands than in the unmanaged stands, these values did not differ significantly in 2014 (Table 1). Indifferent species which are more common in open habitats (group 2.2) were rare in 1997 and completely disappeared from all stands in 2014. The same applies to non-forest species in the managed stands.

The richness and cover of disturbance indicator species was significantly different between all management types in 1997, with the highest values in group selection stands (Table 1, Fig. 4). Since 1997, a strong decrease in species richness and cover of this group
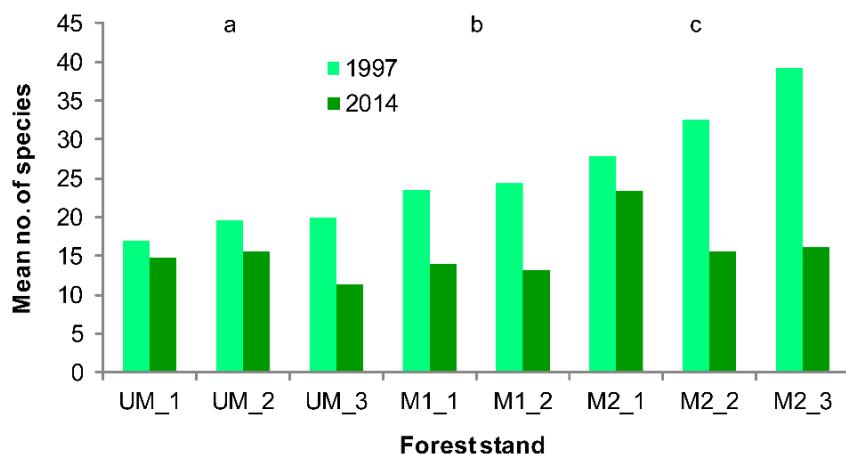
Fig. 2. Mean number of species of the herb layer in 1997 (light green) and 2014 (dark green) in stands of the three management intensity types: UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection harvest; M2, group selection harvest. Numbers after the underscore denote the specific stand (see Supplement E1). Different lower-case letters indicate significant differences among management types (one way ANOVA with post-hoc Tukey's test; $p < 0.05$) in 1997; in 2014: not significant.

Abb. 2. Mittlere Artenzahl in der Krautschicht im Jahr 1997 (hellgrün) und 2014 (dunkelgrün) in Beständen der drei verschiedenen Bewirtschaftungsintensitätstypen: UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme. Zahlen nach dem Unterstrich bezeichnen den einzelnen Bestand (s. Anhang E1). Verschiedene Kleinbuchstaben bezeichnen signifikante Unterschiede zwischen den Bewirtschaftungsintensitätstypen (one-way ANOVA mit post-hoc Tukeys Test; $p < 0,05$) in 1997; in 2014: nicht significant.
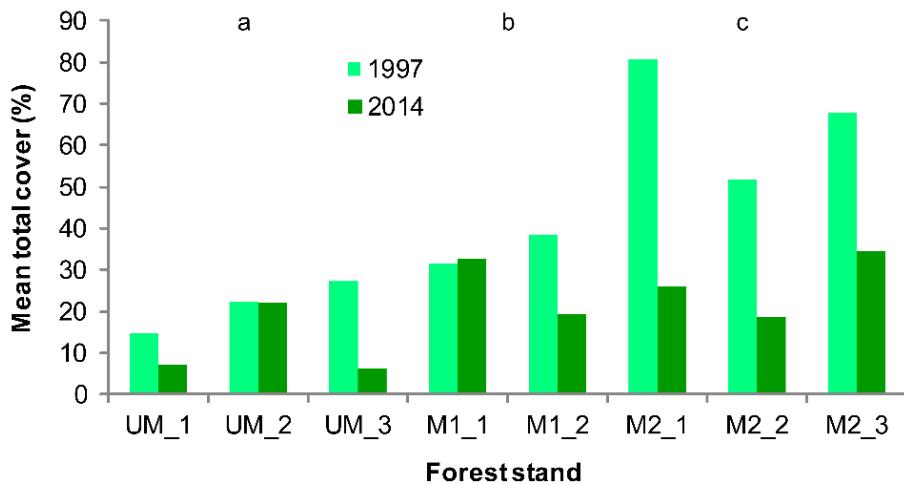
Fig. 3. Mean total cover (in %) of herb layer species in 1997 (light green) and 2014 (dark green) in stands of the three management intensity types. For details see Figure 2.

Abb. 3. Gesamtdeckung (in %) der Krautschichtarten im Jahr 1997 (hellgrün) und 2014 (dunkelgrün) in Beständen der drei verschiedenen Bewirtschaftungsintensitätstypen. Zur Erläuterung s. Abbildung 2.
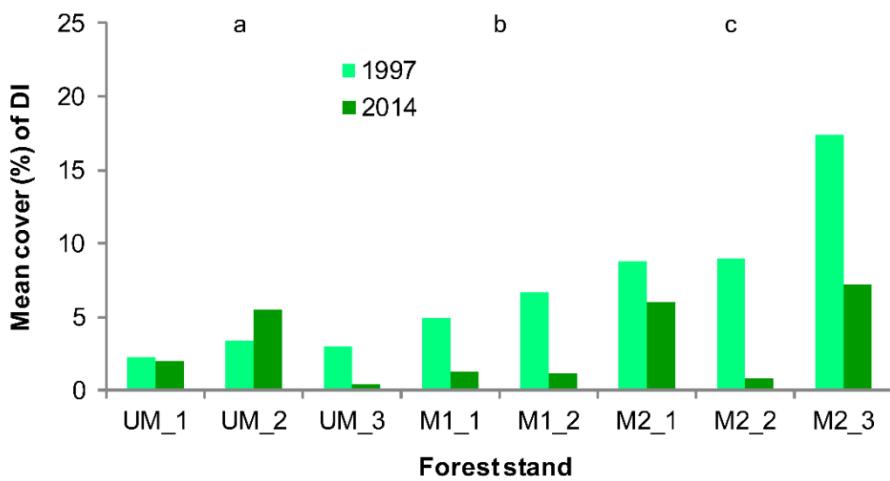
Fig. 4. Mean cover (in %) of disturbance indicator species (DI) in the herb layer in 1997 (light green) and 2014 (dark green) in stands of the three management intensity types. For details see Figure 2.

Abb. 4. Mittlere Deckung der Störzeiger (in %) in der Krautschicht im Jahr 1997 (hellgrün) und 2014 (dunkelgrün) in Beständen der drei verschiedenen Bewirtschaftungsintensitätstypen. Zur Erläuterung s. Abbildung 2.

occurred in all management types. However, disturbance indicator species still depict a considerable proportion (nearly 25%) of all species in the formerly group selection stands. Overall, species richness and cover of disturbance indicators did not differ significantly between management types in 2014.

Table 1. Mean species richness and total cover of the herb layer and of species groups across the management intensity types (UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection; M2, group selection harvest) in the sampling years 1997 and 2014. Species groups according to SCHMIDT et al. (2011): 1.1 strict forest species; 1.2 species of forest edges and clearings; 2.1 indifferent species; 2.2 indifferent species more common in open habitats. DI, disturbance indicators (according to GRABHERR et al. 1998). Asterisks (* $p < 0.05$; ** $p < 0.01$) denote significant effects of management type on response variables, with different lower case letters indicating significant differences among management types.

Tabelle 1. Mittlere Artenzahl und Gesamtdeckung der Krautschicht und der Artengruppen in den verschiedenen Bewirtschaftungsintensitätstypen (UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme) in den Untersuchungsjahren 1997 und 2014. Artengruppen nach SCHMIDT et al. (2011): 1.1 streng waldgebundene Arten; 1.2 Arten der Waldränder und -Lichtungen; 2.1 indifferente Arten; 2.2 indifferente Arten mit Schwerpunkt im Offenland. DI, Störzeiger nach GRABHERR et al. (1998). Verschiedene Kleinbuchstaben bezeichnen signifikante Unterschiede zwischen den Bewirtschaftungsintensitätstypen in den einzelnen Untersuchungsjahren. *P*, Signifikanz gemäß one-way ANOVA mit post-hoc Tukeys Test; ns, nicht signifikant; * $p < 0{,}05$; ** $p < 0{,}01$.

	1997				2014			
	UM	M1	M2	*p*	UM	M1	M2	*p*
Species richness								
All species	18.7a	24.0b	33.2c	*	14.0	13.6	18.4	ns
1.1	13.5a	15.5b	20.2c	**	10.8	9.9	12.7	ns
1.2	0.1a	0.4b	1.3c	**	0.0	0.0	0.1	ns
2.1	5.1	7.8	11.2	ns	3.2	3.7	5.6	ns
2.2	0.1	0.2	0.6	ns	0.0	0.0	0.0	ns
Non-forest	0.0	0.1	0.1	ns	0.0	0.0	0.0	ns
DI	3.9a	6.2b	11.1c	*	2.0	2.0	4.4	ns
Cover (%)								
All species	21.5a	35.1b	66.7c	**	11.8	26.0	26.5	ns
1.1	19.1a	19.5a	44.4b	*	8.2	23.2	19.5	ns
1.2	0.1a	0.2a	3.5b	*	0.0	0.0	< 0.1	ns
2.1	2.3a	15.4b	18.4b	**	3.6	2.8	7.0	ns
2.2	< 0.1	0.1	0.4	ns	0.0	0.0	0.0	ns
Non-forest	0.0	< 0.1	< 0.1	ns	0.0	0.0	0.0	ns
DI	2.9a	5.8b	11.7c	*	2.6	1.2	4.7	ns

3.3 Indicator species analysis

The indicator species analysis for 2014 (Table 2) revealed clear differences in the numbers of species that indicate for a particular management intensity type. *Stellaria holostea* (frequency of 84%) and *Poa nemoralis* (frequency of 21%) proved to be significant and marginally significant, respectively, indicators for unmanaged stands. Furthermore, two species are indicative of the former single-tree selection stands (*Dryopteris dilatata*, *Euonymus europaeus*), both of which with low frequencies of occurrence (33% and 39%, respectively). By contrast, ten species were indicative for (and mostly restricted to) the former group selection managed stands. These species showed a wide range of occurrence frequencies. Seven out of these ten species are strict forest species (group 1.1), while the remaining

Table 2. Results of the indicator species analyses for 2014 (ISA), showing species that significantly indicate for one or two management intensity types (UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection; M2, group selection harvest). IV: Indicator value % (*p* < 0.05); P1: "Presence only in type" evaluates the hypotheses that a species occurs solely in the management intensity type or a combination of two types; FO: "frequency of occurrence" depicts the rate at which a species occurs in the respective management intensity type. Habitat: species' classification according to habitat preference following SCHMIDT et al. (2011) (see Table 1 for explanations); DI: disturbance indicators following GRABHERR et al. (1998). Significance codes: ' *p* < 0.06; * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001.

Table 2. Ergebnisse der Indikatorarten-Analyse für 2014 (ISA); Arten mit signifikanter Indikator-Funktion für eine oder zwei Bewirtschaftungsintensitätstypen (UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme). IV, Indikator-Wert in % (*p* < 0,05); P1: Präsenz in nur einem Bewirtschaftungsintensitätstyp oder in einer Kombination aus zwei Typen; FO: Vorkommens-Frequenz in dem jeweiligen Bewirtschaftungsintensitätstyp. Habitat: Klassifikation nach SCHMIDT et al. (2011) (s. Tab. 1); DI: Störzeiger nach GRABHERR et al. (1998). Significanzcodes: ' *p* < 0,06; * *p* < 0,05; ** *p* < 0,01; *** *p* < 0,001.

	IV	P1	FO	Habitat	DI
UM					
Stellaria holostea	81*	0.78	0.84	1.1	
Poa nemoralis	46'	1.0	0.21	1.1	
M1					
Dryopteris dilatata	56**	0.96	0.33	1.1	
Euonymus europaeus juv.	56'	0.8	0.39	2.1	
M2					
Carpinus betulus juv.	78*	0.78	0.78	1.1	
Rubus idaeus	76**	0.87	0.67	1.2	X
Circaea lutetiana	75*	0.67	0.83	1.1	
Carex remota	71**	0.82	0.61	1.1	X
Urtica dioica	67**	1.00	0.44	2.1	X
Stellaria nemorum	53*	0.85	0.33	1.1	
Festuca altissima	52*	0.98	0.28	1.1	
Ulmus glabra juv.	47*	1.00	0.22	1.1	
Juncus effusus	41'	1.00	0.17	2.1	X
Impatiens noli-tangere	41'	1.00	0.17	1.1	
UM + M2					
Galium odoratum	88**	0.89	0.86	1.1	
Carex sylvatica	79*	0.92	0.68	1.1	
M1 + M2					
Acer pseudoplatanus juv.	93***	1.00	0.87	1.1	
Melica uniflora	91***	0.92	0.90	1.1	
Dryopteris filix-mas	82**	0.97	0.70	1.1	
Athyrium felix-femina	73*	0.93	0.57	1.1	

three species are typical of forest clearings and edges (*Rubus idaeus*, group 1.2) or indifferent generalists (*Urtica dioica*, *Juncus effusus,* group 2.1). Furthermore, four species are classified as disturbance indicators (*Rubus idaeus*, *Urtica dioica*, *Carex remota* and *Juncus effuses*, with the latter two being indicators for soil compaction and water logging). Four species proved to be indicators for both types of managed stands (Table 2) and are strict forest species (group 1.1).

Comparing the results of the indicator species analysis for all species between 1997 and 2014, the number of species indicative for managed stands decreased considerably: from five to two indicator species for former single-tree selection stands (*Aegopodium podagraria*, *Corylus avellana*, *Filipendula ulmaria*, *Rubus caesius*, *Sanicula europaea*), and from 21 to ten indicator species for former group selection managed stands. Losses were particularly obvious for species with (very) low frequencies in 1997. Most of these species are classified as disturbance indicators. Simultaneously, a substantial decrease in the frequencies of species such as *Geranium robertianum* (-25%), *Impatiens parviflora* (-18%), *Epilobium montanum* (-11%), *Juncus effusus* (-33%) and *Urtica dioica* (-19%) occurred in both managed stand types. *J. effusus* and *U. dioica* disappeared completely from former single-tree selection stands. Constant frequencies of disturbance indicators over time were found only for *Carex remota* and *Equisetum sylvaticum*, both of which are indicative for soil compaction and water logging. Furthermore, constant frequencies of occurrence were observed for strict forest species such as *Milium effusum* or *Circaea lutetiana* and tree species regeneration.

3.4 Light availability and Ellenberg indicator values

Mean LAI values showed a decreasing trend with increasing management intensity, which was, however, not statistically significant (Table 3). This was due to a high variance in LAI records obtained from the former group selection stands (stand mean values of 3.4, 4.1 and 5.4) compared to similar values found in the former single-tree selection stands (4.9 and 5.3) and in the unmanaged stands (5.3, 5.5 and 5.6). Accordingly, the highest SEL values were recorded in former group selection stands, reflecting a high heterogeneity in light availability at the plot level. In addition, we found a significant increase of the moisture values (F) with increasing management intensity, whereas indicator values for soil reaction (R) and nutrient availability (N) remained unchanged.

3.5 Correlation analysis

Management intensity was significantly positively correlated with total species richness and cover of the herb layer (Table 4). Likewise, positive correlations were found between management intensity and richness of indifferent species and disturbance indicators as well as for the cover of strict forest species and indifferent species. The cover of the tree layer was not significantly correlated to the species data. Highly significant negative correlations were observed for LAI and all the species data. By contrast, Ellenberg light values were only significantly positively correlated with the total number of species as well as with the species richness and cover of indifferent species and disturbance indicators. Furthermore, a positive association was found for moisture values and species richness and cover (with the exception of the species richness of strict forest species).

Table 3. Means of unweighted Ellenberg indicator values, LAI and SEL (%) values for the management intensity types (UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection; M2, group selection harvest) in 2014. Unweighted Ellenberg indicator values: L, light value; F, moisture value; R, soil reaction; N, nutrient supply. LAI, leaf area index; SEL, standard error of LAI. Asterisks (* $p < 0.05$; ** $p < 0.01$) denote significant effects of management type on response variables, with different lower case letters indicating significant differences among management types.

Table 3. Mittlere ungewichtete Zeigerwerte nach Ellenberg (L, Lichtgenuss; F, Feuchtigkeit; R, Bodenreaktion; N, Stickstoffversorgung), Blattflächenindex (LAI) und Standardfehler des Blattflächenindex (SEL) in den drei verschiedenen Bewirtschaftungsintensitätstypen (UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme) in 2014. Verschiedene Kleinbuchstaben bezeichnen signifikante Unterschiede zwischen den Bewirtschaftungsintensitätstypen in den einzelnen Untersuchungsjahren. *P*, Signifikanz gemäß one-way ANOVA mit post-hoc Tukeys Test; ns, nicht signifikant; * $p < 0,05$; ** $p < 0,01$.

	UM	M1	M2	*p*
LAI	5.5	5.1	4.4	ns
SEL	0.11a	0.19b	0.28c	*
L	3.8	3.9	4.0	ns
F	5.3a	5.5b	5.7c	*
R	6.1	5.8	5.9	ns
N	5.6	5.7	5.8	ns

4. Discussion

The findings of this study revealed in both types of former forest management intensity a tendency of the herb layer to approximate the community composition of the unmanaged reference stands, supporting the conclusion of VON OHEIMB & HÄRDTLE (2009), that low-intensity single-tree selection management has little influence on herb layer biodiversity and community composition. A strong recovery of herb layer communities towards the forest vegetation associated with unmanaged stands was observed in the former single-tree selection stands. Even though the mean values of herb layer richness and coverage of formerly more intensively managed stands (i.e., former group selection harvest) did not differ significantly compared to the unmanaged stands, indicator species analysis revealed that certain compositional differences still remain. The unmanaged, near-natural reference stands exhibited a relatively stable herb layer typical of beech-dominated forests in the climax phase.

Several studies identified clearly positive correlations between vascular plant species diversity and anthropogenic disturbance intensity linked with forest management (MEYER & SCHMIDT 2008, PAILLET et al. 2010, SCHMIDT & HEINRICHS 2012, SCHMIDT 2013). This has been explained by enhanced resource availability and habitat diversification in deciduous forests which are naturally relatively poorly structured (STANDOVÁR 1998, SCHMIDT & HEINRICHS 2012, SCHMIDT 2013, HEINRICHS & SCHMIDT 2016). In our study, the tree layer coverage and beneath-canopy light conditions became more similar to the conditions in the unmanaged stands over time (non-significant differences in LAI values in 2014). Due to the high crown plasticity of *Fagus sylvatica* (SCHRÖTER et al. 2012) as well as natural tree regeneration, small canopy gaps created by single-tree die-back or single-tree selection cutting in beech-dominated forests can be occupied in a relatively short time (BRUNET et al. 2010). However, a high variation in the LAI values together with significantly higher SEL values

Table 4. Pearson's product-moment correlation for species richness and cover data of the herb layer, management intensity and environmental parameters in 2014. MT, management intensity type, ordered as UM < M1 < M2 (UM, unmanaged; M, managed with different intensities until 1994: M1, single-tree selection harvest; M2, group selection harvest); LAI, leaf area index; SEL, standard error of LAI. Unweighted Ellenberg indicator values: L, light value; F, moisture value; R, soil reaction; N, nutrient supply. Species groups according to SCHMIDT et al. (2011): 1.1 strict forest species; 2.1 indifferent species. DI, disturbance indicators (according to GRABHERR et al. 1998). ns, non significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 4. Pearson's product-moment Korrelation für Artenzahlen und Deckungsgrad-Daten, Bewirtschaftungsintensität und Standortdaten in 2014. MT, Bewirtschaftungsintensitätstypen, geordnet nach: UM < M1 < M2 (UM, unbewirtschaftet; M, bewirtschaftet mit unterschiedlicher Intensität bis 1994: M1, Einzelbaum-Entnahme; M2, Gruppen-Entnahme); LAI, Blattflächenindex; SEL, Standardfehler des LAI. Ungewichtete Ellenberg-Zeigerwerte: L, Lichtgenuss; F, Feuchtigkeit; R, Bodenreaktion; N, Stickstoffversorgung. Artengruppen nach SCHMIDT et al. (2011): 1.1 streng waldgebundene Arten; 2.1 indifferente Arten. DI, Störzeiger (nach GRABHERR et al. 1998). ns, nicht signifikant; * $p < 0,05$; ** $p < 0,01$; *** $p < 0,001$.

Herb layer	MT	Cover tree layer	LAI	SEL	L	F	R	N
Species richness								
All species	0.36*	ns	-0.47***	0.31*	0.32*	0.41**	ns	ns
1.1	ns	ns	-0.32*	ns	ns	ns	ns	ns
2.1	0.42**	ns	-0.55***	0.34*	0.34*	0.49***	ns	ns
DI	0.44**	ns	-0.59***	0.31*	0.32*	0.52***	ns	ns
Cover								
All species	0.46***	ns	-0.44**	0.32*	ns	0.57***	ns	ns
1.1	0.43**	ns	-0.36*	0.31*	ns	0.49***	ns	ns
2.1	0.29*	ns	-0.40**	ns	0.32*	0.47**	ns	ns
DI	ns	ns	-0.40**	ns	0.35*	0.43**	ns	ns

point at the existence of more heterogeneous site conditions and niche diversification in the former group selection stands. Diversification in habitat conditions may result from interplays of harvest-related canopy opening, topsoil layer injury, litter removal and soil compaction (PAILLET et al. 2010, WELTECKE & GAERTIG 2011, SCHMIDT & HEINRICHS 2012, EBELING et al. 2016). These anthropogenic changes in the forest environment may explain improved resource availability with regard to higher light, water and nutrient values in managed stands.

Similar to occasional, large-scale natural disturbances, former group selection harvesting could also accelerate biotic mineralization by decaying downed wood debris and higher temperatures due to higher radiation amounts reaching the forest floor of the thinned stands (COLLINS & PICKETT 1988, SCHMIDT & HEINRICHS 2012). Furthermore, reduced root suction due to tree extraction could explain for higher soil moisture in managed stands (SCHIEBER & JANÍK 2012, SCHMIDT & HEINRICHS 2012) and for elevated mineralization rates. The enhanced resource availability may have reduced inter-specific competitive pressure in the herb layer (HÄRDTLE et al. 2003). Simultaneously, it facilitates the establishment of heliophilous, nitrophilous and hydrophilous species leading to a pronounced change in the forest species pool (RÖDER et al. 1996, FISCHER et al. 2009, SCHMIDT & HEINRICHS 2012). Furthermore, litter removal and top soil disturbances were reported to enable the germination

and establishment of ruderal annuals like *Impatiens parviflora*, late-flowering grasses like *Carex remota, Juncus effusus* and heliophilous forbs like *Urtica dioica,* either by activating their diaspores from the forest seed bank (FISCHER et al. 2009, SCHMIDT & HEINRICHS 2012) or by inducing the germination of otherwise introduced diaspores on the bare mineral soil (HÄRDTLE et al. 2003). As VON OHEIMB & HÄRDTLE (2009) found in the assessment of 1997, management-related impacts on the herb layer were most evident in substantially disturbed clearings. In 2014, such gaps might still harbour relatively high species numbers. However, canopy gap closure by tree regeneration after disturbances has been widely report-ed in the literature (HUSS & BUTLER-MANNING 2006, KATHKE & BRUELHEIDE 2010, SCHMIDT & HEINRICHS 2012, SCHMIDT 2013). In the managed stands, dense tree regenera-tion (see shrub layer cover values) created light-deprived conditions in the understorey, resembling those in unmanaged stands and excluding many light-demanding species. As a result, the species richness considerably declined in the former group selection stands. Ruderal generalists and disturbance indicators persisted mainly in the remaining clearings, particularly on logging trails. This may explain the low, but still observable presence of species of forest edges and clearings in group selection stands.

In contrast, unmanaged stands exhibited small changes in community composition of the herbaceous layer. In line with findings on increasing canopy closure and homogenisation of canopy species after management cessation (MEYER & SCHMIDT 2008, FISCHER et al. 2009, SCHMIDT 2013, MÖLDER et al. 2014), no major changes in the herb layer composition were found since 1997. Similar observations were reported by SCHIEBER & JANÍK (2012). The relatively stable state of the upper tree layer and the species-poor herb layer may be ex-plained by persisting phase-synchronization to the climax phase (STANDOVÁR 1998). In terms of this synchronization to even-aged cohorts, previous management still exerts an impact on herb layer vegetation. The poor horizontal and vertical structural diversity of the unmanaged stands results in a decrease in light and nutrient availability, and a consequently narrow habitat range. High litter thickness is considered to hinder the establishment of tree regeneration and of many herbaceous species, thus, reducing their diversity (MEYER & SCHMIDT 2008, MÖLDER et al. 2008). Only few species that have adapted to such extreme conditions in their phenology (such as geophytes) and morphology (i.e., species with creep-ing clonal growth) can colonize the forest floor (SEEBACHER et al. 2012). If disturbance indicators such as *Deschampsia cespitosa* or *Poa trivialis* occurred punctually, they exhibit-ed very poor vitality, which is consistent with observations of SCHIEBER & JANÍK (2012). Overall, the herb layer patterns of unmanaged stands did not substantially change since 1997.

5. Conclusions

Our study provides evidence that the forest herb layer sensitively reflects the impacts of forest management measures differing in intensity and time scale, provided that floristic assessments consider the habitat and ecological requirements of the species analyzed (in-stead of pure richness or diversity measurements). Despite the well-known low dispersal power of many forest herb species, species assemblages can shift within decadal scales in response to the management measures applied. The herb layer species composition associat-ed with low-intensity measures resembles those of long-term unmanaged stands, with a lower number of total species per area unit but a (relatively) high number of typical forest species. In contrast, high-intensity measures exhibit a higher total number of herb layer

species, but in many cases associated with increasing proportions of disturbance indicators or open-landscape species. In managed beech forest ecosystems, management systems minimizing interventions (such as single-tree selection) may, thus, contribute to the long-term protection of a typical herb layer species composition in terms of both species richness and abundance. However, the natural disturbance regime in this forest type may also include occasional larger-scale disturbances such as wind storms or snow break events, and by this the creation of large canopy gaps (HOBI et al. 2015). This initiates important successional pathways, including the appearance of early- and mid-successional plant species, and has to be included in nature-oriented management approaches. This requires both, the establishment of local unmanaged "reference areas" where natural forest dynamics are allowed to take place, and strategies how to deal with such disturbances once they occur in the managed forests (e.g., leaving some disturbed forest patched unmanaged; FISCHER 2011).

Erweiterte deutsche Zusammenfassung

Einleitung – Wälder sind bedeutende Refugien für viele hochspezialisierte Arten. In Mitteleuropa kann jedoch nur ein Bruchteil der rezenten Wälder noch als naturnah oder ‚ursprünglich' gelten. Da die bestehenden Waldschutzgebiete unzureichend für einen großflächigen Artenschutz sind (MEYER & SCHMIDT 2008), ist eine Vereinbarkeit von nachhaltiger Forstwirtschaft und Naturschutz in bestehenden Waldgebieten anzustreben. Eine naturnahe Forstwirtschaft sollte dabei den Schutz natürlicher Prozesse und die Nachahmung natürlicher Strukturdynamik beinhalten. In mitteleuropäischen Buchenwäldern wird die Artenvielfalt der Bodenvegetation durch Bewirtschaftung eher noch erhöht (PAILLETT et al. 2010), während lange Zeit unbewirtschaftete Buchenwälder und Buchen-Urwälder – hinsichtlich der Gefäßpflanzen – als vergleichsweise artenarm gelten. Die vorliegende Studie untersuchte die langzeitlichen Auswirkungen einer verringerten Intensität in der Waldbewirtschaftung auf die Krautschichtvegetation von Buchen- und Buchenmischwäldern im Vergleich zu vormals unterschiedlich bewirtschafteten (Einzelstamm-Entnahme oder Gruppen-Nutzung) und ungenutzten, naturnahen Beständen vergleichbarer Standorte. Hierbei sollten die Hypothesen getestet werden, dass (1) die Krautschicht in den bewirtschafteten Beständen über die Zeit bezüglich der Artenvielfalt und -zusammensetzung eine Annäherung an die Verhältnisse in den unbewirtschafteten Beständen zeigt, und (2) dass die Veränderungen in Wäldern mit vormals höherer Bewirtschaftungsintensität (Gruppen-Entnahme) stärker ausfallen als in denjenigen mit vormals geringerer Bewirtschaftungsintensität (Einzelstamm-Entnahme).

Material und Methoden – Im Untersuchungsgebiet des Lübecker Stadtwaldes wurden Bestände von Tieflands-Buchenwäldern und -Buchenmischwäldern (*Galio-Fagetum*, mesotraphente Buchen-Eichen-Bestände, *Stellario-Carpinetum*) untersucht. Auf der Grundlage einer Erstaufnahme von 1997 (VON OHEIMB 2003) wurden im Jahr 2014 Wiederholungsaufnahmen auf quasi-permanenten Dauerbeobachtungsflächen (200 m²) durchgeführt. In der früheren Studie wurden zwei verschiedene Bewirtschaftungsintensitäten unterschieden: Einzelstamm-Entnahme (geringe Intensität) und Gruppen-Nutzung (mittlere Intensität). Seit 1994 unterliegen alle bewirtschafteten Bestände einem einheitlichen, naturnahen Bewirtschaftungs-System (Naturland-, FSC-Zertifizierung). Als unbewirtschaftete Referenz dienten jeweils Flächen im Teilgebiet „Schattin", die seit den 1950er Jahren keiner geregelten Bewirtschaftung mehr unterlagen und seit 1994 als unbewirtschaftete Referenzfläche ausgewiesen sind. Die Abundanz der Arten der Krautschicht (Krautige, juvenile Gehölze) wurde in % geschätzt. Begleitend wurde der Lichteinfall unter den Kronen als Blattflächen-Index (LAI) sowie die Variabilität der Kronendeckung der Bestände als Standardfehler des LAI (SEL) gemessen.

Die abiotischen Standortbedingungen wurden zudem näherungsweise durch die Berechnung ungewichteter Ellenberg-Zeigerwerte bestimmt. Unterschiede zwischen den drei verschiedenen Bewirtschaftungsintensitätstypen (UM, unbewirtschaftet; M1, bis 1994 mit Einzelstamm-Entnahme bewirtschaftet; M2, bis 1994 mit Gruppen-Entnahme bewirtschaftet) wurden auf ihre statistische Signifikanz getestet.

Ergebnisse –Zwischen den Bewirtschaftungsintensitätstypen wurden im Jahr 2014 keine signifikanten Unterschiede bezüglich Artenzahlen und Deckungsgraden sowohl aller Arten als auch bestimmter Artengruppen festgesellt. Nur wenige Arten zeigten eine deutliche Bindung an unbewirtschaftete oder ehemals mit geringer Intensität bewirtschaftete Bestände. Hingegen fanden sich noch 10 Arten, die einen deutlichen Schwerpunkt im Vorkommen in den ehemals mit mittlerer Intensität bewirtschafteten Beständen aufwiesen. Der Anteil an Störzeigern ist im Vergleich zu 1997 in allen Beständen stark zurückgegangen, lediglich einzelne Arten in geringer Deckung waren 2014 in den vormals in Gruppen-Nutzung bewirtschafteten Beständen vorhanden. Bewirtschaftete Bestände (M1, M2) waren in der Tendenz lichter als die unbewirtschafteten Bestände.

Diskussion – Die Ergebnisse zeigen eine bemerkenswerte Annäherung der Vegetation von ehemals unterschiedlich intensiv bewirtschafteten Beständen an diejenige der naturnahen, ungenutzten Waldbestände. Dies geht mit einer Abnahme der Artenvielfalt einher, die jedoch insbesondere in einer Abnahme der Störzeiger begründet ist. Die Zusammensetzung der Krautschicht wird daher zunehmend von streng waldgebunden Arten dominiert. Während die ehemals in Gruppen-Nutzung bewirtschafteten Bestände nach der Verringerung der Bewirtschaftungsintensität die stärksten Veränderungen zeigen, ist in den unbewirtschafteten, naturnahen Beständen seit 1997 keine deutliche Veränderung feststellbar. Verbleibende Unterschiede in der Artenzusammensetzung (insbes. geringe Präsenz von Störzeigern) kann auf die anhaltenden Auswirkungen früherer Kronenauflichtung und Bodenstörungen (insbes. Freilegung des Mineralbodens, Verdichtung in Fahrspuren) zurückgeführt werden. Aber auch in den ehemals intensiver bewirtschafteten Beständen der Kategorie M2 führt die zunehmende Naturverjüngung zu immer schattigeren Verhältnissen, wodurch lichtbedürftige Arten allmählich von Schattentoleranten Waldarten verdrängt werden.

Schlussfolgerungen – Basierend auf einem Langzeitvergleich von 1997 und 2014 können Einschätzungen zu den Auswirkungen extensiver und mittel-intensiver Waldbewirtschaftung auf die Krautschicht von Buchen- und Buchenmischwäldern gegeben werden. Hierbei zeigt sich insgesamt eine quantitative Abnahme des Artenreichtums der Krautschicht, wobei zugleich eine Näherung zu einer vergleichsweise artenarmen, aber waldtypischen Phyotocoenose erfolgte. Eine naturnahe, extensive Bewirtschaftung nach dem Prozessschutz-Konzept ist daher geeignet, eine naturnahe, waldtypische Krautschicht zu erhalten und genügt somit Anforderungen des Naturschutzes.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Stand characteristics of the eight surveyed stands of three forest types, arranged in order of increasing harvest intensity.

Anhang E1. Bestandesdaten der acht untersuchten Waldbestände in drei verschiedenen Bewirtschaftungsintensitätstypen.

Supplement E2. Vegetation relevés of the eight surveyed stands from the year 1997.

Anhang E2. Vegetationsaufnahmen der acht untersuchten Waldbestände aus dem Jahr 1997.

Supplement E3. Vegetation relevés of the eight surveyed stands from the year 2014.

Anhang E3. Vegetationsaufnahmen der acht untersuchten Waldbestände aus dem Jahr 2014.

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Petzold et al.: Effects of forest management intensity on herb layer diversity and composition of deciduous forests

Supplement E1. Stand characteristics of nine surveyed stands of three forest types, arranged in order of increasing harvest intensity. Data obtained from von Oheimb & Härdtle (2009) and the forest inventory of 2004. MT, management intensity type; VH, volume of timber harvested (VH is given as m^3 ha^{-1} year^{-1}); FH, frequency of harvest operations (FH as number of harvest interventions from 1980 to 1997). UTL, cover (%) of upper tree layer; SL, cover of shrub layer. N, number of plots per stand.

Anhang E1. Bestands-Daten der 9 untersuchten Waldbestände in 3 verschiedenen Bewirtschaftungsformen, geordnet nach Bewirtschaftungsintensität. Daten nach von Oheimb & Härdtle (2009) und Forsteinrichtungs-Daten von 2004. MT, Bewirtschaftungsform; VH, entnommener Bestandsvorrat (m^3 Holz ha^{-1} year^{-1}); FH, Frequenz der Entnahmen (Anzahl der Eingriffe von 1980 bis 1997). UTL, Deckung (%) der oberen Baumschicht; SL, Deckung der Strauchschicht. N, Anzahl Plots pro Bestand.

Overstorey composition[1]	Age (year)	MT[2]	VH[3]	FH	UTL	SL	Water balance	Nutrient supply	Soil type	N
Mesotrophic beech forests										
Fs(88),Qr(7),o(5)	120	UM			87.5	0.2	fresh	good	Pseudogley, boulder glay	6
Fs(71),Qr(15),Fe(3),o(11)	123	M2	7.5	5	60	36.7	fresh	good	Pseudogley, boulder glay	6
Fs(89),Qr(7),Fe(4)	126	M2	8.4	3	64	16	fresh	good	Pseudogley, boulder glay	5
Oak-hornbeam forest										
Qr(43),Fs(29),Cb(24),o(4)	191	UM			86.7	0.3	fresh	good	Pseudogley, boulder glay	6
Qr(85),Fs(8),Cb(3),o(4)	144	M1	2.5	6	61.7	15.5	fresh	good	Pseudogley, boulder glay	6
Qr(71),Fs(15),Fe(9),Cb(2)	213	M1	17.2	3	71.7	13.3	fresh	good	Pseudogley, boulder glay	6
Mesotrophic beech-oak forests										
Fs(52),Qr(20),Cb(20),o(8)	122	UM			83.6	6	fresh	good	Pseudogley, boulder glay	7
Fs(65),Qr(20),Fe(12),o(3)	127	M1	1.3	3	75	3.8	fresh	good	Pseudogley, boulder glay	6
Fs(54),Qr(36),Fe(9),o(1)	138	M2	17.6	7	53.3	29.2	fresh	good	Pseudogley, boulder glay	6

Petzold et al.: Effects of forest management intensity on herb layer diversity and composition of deciduous forests

Supplement E2. Vegetation relevés of the eight surveyed stands from the year 1997. Type: UM: unmanaged; M1: single-tree selection harvest; M2: group selection harvest
Anhang E2. Vegetationsaufnahmen der acht untersuchten Waldbestände aus dem Jahr 1997. Type: UM: unbewirtschaftet, M1: Einzelbaum-Entnahme; M2: Gruppen-Entnahme.

	Species group	Tree / Shrub / Herb cover values per relevé
Type		UM (Nr. 23–30, 1–20), M1 (Nr. 21, 22, 31–50), M2 (Nr. 51–85)
Number		23 24 25 26 27 28 29 30 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 64 65 66 67 68 69 70 71 72 73 74 53 54 55 56 57 58 59 60 61 62 63 75 76 77 78 79 80 81 82 83 84 85
Tree layer cover		90 90 90 90 90 100 95 90 90 90 95 90 90 80 90 95 95 95 90 85 85 95 100 95 95 95 90 100 100 100 90 95 90 100 100 95 100 95 100 90 80 90 90 95 100 80 105 95 100 80 60 25 30 20 45 30 20 45 50 45 50 ...
Shrub layer cover		0 0 0.5 0 0 0 0 1 0 1 12 1 5 1 5 1 5 15 0 1 2 3 0 0 1 2 2 0 3 0 2 0 2 0 30 25 25 25 8 35 30 20 5 25 10 0.5 3 15 25 3 6 0 0 0 45 30 8 25 30 6 4 40 45 30 0 1 5 25 0 30 8 50 40 40 8 25 5
Herb layer cover		6 7 10 14 14 7 5 6 6 12 14 29 45 22 2 7 9 2 4 6 3 10 58 75 7 12 8 11 9 10 4 39 24 10 19 11 39 11 67 25 7 36 35 7 32 20 19 48 44 19 10 15 21 57 78 54 25 59 70 39 5 24 28 31 47 29 29 43 20 37 25 54 18 57 38 25 50 30 52 44 32 40 51 36 28

Herb layer

Species name	Species group
Acer campestre	2.1
Acer platanoides	2.1
Acer pseudoplatanus	2.1
Aegopodium podagraria	2.1
Aesculus hippocastanum	2.2
Agrostis capillaris	2.1
Ajuga reptans	2.1
Alliaria petiolata	2.1
Athyrium filix-femina	1.1
Brachypodium sylvaticum	1.1
Calamagrostis canescens	2.1
Calamagrostis epigejos	2.1
Cardamine flexuosa	1.2
Carex muricata	2.1
Carex pallescens	2.1
Carex pilulifera	2.1
Carex remota	1.1
Carex sylvatica	1.1
Carpinus betulus	1.1
Chrysosplenium alternifolium	1.1
Circaea lutetiana	1.1
Cirsium arvense	2.2
Corylus avellana	2.1
Crataegus laevigata agg.	2.1
Crataegus monogyna	2.1
Crepis paludosa	2.1
Dactylis glomerata	2.2
Deschampsia cespitosa	2.1
Deschampsia flexuosa	2.1
Dryopteris carthusiana	1.1
Dryopteris dilatata	1.1
Dryopteris filix-mas	1.1
Elymus caninus	1.1
Epilobium angustifolium	1.2
Epilobium montanum	2.1
Epilobium parviflorum	non-forest
Epipactis helleborine	1.1
Equisetum arvense	2.1
Equisetum sylvaticum	1.1
Euonymus europaea	2.1
Fagus sylvatica	1.1
Festuca altissima	1.1
Festuca gigantea	1.1
Festuca rubra	2.2
Filipendula ulmaria	2.2
Frangula alnus	2.1
Fraxinus excelsior	2.1
Galeopsis bifida	2.1
Galeopsis tetrahit	2.1
Galium aparine	2.1
Galium odoratum	1.1
Geranium robertianum	1.1
Geum urbanum	2.1
Glechoma hederacea	2.1
Hedera helix	1.1
Heracleum sphondylium	2.2
Hieracium lachenalii	2.1
Holcus lanatus	2.2
Ilex aquifolium	1.1
Impatiens noli-tangere	1.1
Impatiens parviflora	1.1
Juncus effusus	2.1
Lamium galeobdolon	1.1
Lonicera periclymenum	2.1
Luzula campestris	2.1
Luzula pilosa	1.1
Maianthemum bifolium	1.1
Melica uniflora	1.1
Milium effusum	1.1
Moehringia trinervia	2.1
Oxalis acetosella	1.1
Persicaria maculosa	non-forest
Phyteuma spicatum	1.1
Poa nemoralis	1.1
Poa trivialis	2.1
Polygonatum multiflorum	1.1
Primula elatior	1.1
Prunus avium	2.1
Prunus padus	2.1
Prunus spinosa	2.1
Pseudotsuga menziesii	1.1
Pteridium aquilinum	1.1
Pulmonaria obscura	1.1
Quercus robur	2.1
Quercus rubra	1.1
Ranunculus lanuginosus	1.1
Ranunculus repens	2.1
Ribes uva-crispa	2.1
Rosa spec.	2.1
Rubus caesius	2.1
Rubus fruticosus agg.	2.1
Rubus idaeus	1.2
Rumex obtusifolius	non-forest
Rumex sanguineus	2.1
Sambucus nigra	2.1
Sanicula europaea	1.1
Scrophularia nodosa	2.1
Scutellaria galericulata	2.1
Senecio sylvaticus	2.1
Sorbus aucuparia	2.1
Stachys sylvatica	1.1
Stellaria holostea	1.1
Stellaria media	2.2
Stellaria nemorum	1.1
Tanacetum vulgare	non-forest
Taraxacum officinale agg.	2.1
Taxus baccata	1.1
Ulmus glabra	1.1
Urtica dioica	1.1
Veronica montana	1.1
Viburnum opulus	2.1
Vicia sepium	2.1
Viola reichenbachiana	1.1
Viola riviniana	1.1

Supplement E3. Vegetation relevés of the eight surveyed stands from the year 2014. Type: UM: unmanaged; M1: single-tree selection harvest; M2: group selection harvest

Anhang E3. Vegetationsaufnahmen der acht untersuchten Waldbestände aus dem Jahr 2014. Type: UM: unbewirtschaftet; M1: Einzelbaum-Entnahme; M2: Gruppen-Entnahme.

Species name	Species group	1 UM_1	2 UM_1	3 UM_1	4 UM_1	5 UM_1	6 UM_1	7 UM_2	8 UM_2	9 UM_2	10 UM_2	11 UM_2	12 UM_2	13 UM_2	14 UM_3	15 UM_3	16 UM_3	17 UM_3	18 UM_3	19 UM_3	20 M1_1	21 M1_1	22 M1_1	23 M1_1	24 M1_1	25 M1_1	26 M1_1	27 M1_2	28 M1_2	29 M1_2	30 M1_2	31 M1_2	32 M2_1	33 M2_1	34 M2_1	35 M2_1	36 M2_1	37 M2_1	38 M2_2	39 M2_2	40 M2_2	41 M2_2	42 M2_2	43 M2_2	44 M2_3	45 M2_3	46 M2_3	47 M2_3	48 M2_3	49 M2_3
Tree layer cover		90	70	80	90	90	80	85	90	80	90	90	80	90	80	85	90	90	90	90	90	60	80	70	70	80	70	70	40	70	50	70	50	40	60	60	90	60	80	70	70	60	90	60	70	70	50	40	50	40
Shrub layer cover		8	15	2	0	5	2	10	1	0	0	0.5	0	0	1	0	0	0	0	0	0	0	0	6	2	15	0	20	20	15	8	30	50	70	60	0	20	20	8	30	2	5	5	30	20	10	5	80	20	40
Herb layer cover		11	3	4	4	4	22	4	27	37	29	12	12	14	4	5	6	8	5	9	25	26	16	56	32	42	8	31	6	30	17	23	23	11	24	33	40	25	12	15	17	16	16	37	40	57	52	10	34	16

Herb layer

Species name	Species group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Acer campestre	2.1			0.1	0.1									0.1																																				
Acer pseudoplatanus	2.1			0.1	0.5	0.1	0.1			0.1	0.1				0.1	0.1	0.1	0.1			20	15	10	30	25	10	2	4	1	10	6	10	1	3	10	2	8	8	3	2	5	4	8	20	0.1				5	
Aegopodium podagraria	2.1																											0.1																						
Athyrium felix-femina	1.1	0.1					0.1	0.1	0.5	1		0.1										0.5	1		3	0.1	0.5	0.5		0.5	0.5	4									0.1			0.1	1		0.5	6	1	1
Brachypodium sylvaticum	1.1																											0.5													0.5	0.1	0.1		3					
Calamagrostis epigeios	2.1																																							8										
Carex pilulifera	2.1						0.1																																											
Carex remota	1.1										0.5										0.1	0.1				0.5								0.1		0.5	4	0.5	0.1			0.5			0.1	0.1	0.5	0.1	0.5	
Carex sylvatica	1.1	0.1	0.1		0.1	0.1	0.5	0.1	0.1	1	0.5	0.5	0.1	0.5		0.1		0.1	0.1		0.1	0.1			0.1	1			0.1				0.1	1							0.1	5	4	0.5		2			2	4
Carpinus betulus	1.1	0.1	0.1	0.1	0.1		0.5	0.1				0.1	0.1											2		0.5		0.1	0.5	0.1	1	1.5	1	2	8	2					0.1		1	2	0.5	0.1	1	0.5	0.5	
Circaea lutetiana	1.1	0.5	0.1				0.5	1	1	1		2	3									0.5			1	1		0.1	1	0.5	1	1	0.5		1	2	0.5	1		0.5	4	4	3		4	2				
Corylus avellana	2.1																								0.1						0.5																			
Crataegus laevigata	2.1						0.1									0.1										0.1				0.1										0.1						0.1		1		
Deschampsia cespitosa	2.1		0.1			0.1	0.5	0.1		0.5	0.5	5		0.1				0.1		0.5			1		0.5	0.1		0.5						0.5	0.1	1		3	0.1		0.5	0.5	0.5		0.5	6	4	0.5	0.5	0.5
Dryopteris dilatata	1.1														4			2		1		0.1														0.5														
Dryopteris filix-mas	1.1								0.5			0.5	0.1			0.1				0.1	0.1	2	10	0.1		1		0.5	3				3	0.5	0.5		0.5	0.5	0.1	0.5	0.5		0.5	0.5	0.5	0.5			0.5	
Elymus caninus	1.1																																																	0.5
Epilobium montanum	2.1																									0.1																							0.1	
Epipactis helleborine	1.1																									0.1																								
Equisetum sylvaticum	1.1																0.1																		0.1		0.1									0.5	1			
Euonymus europaeus	2.1		0.1			0.1				0.1												0.5		1		0.1		3		0.5											0.1	0.5							1	0.1
Fagus sylvatca	1.1	0.5	0.5	0.1	0.5	0.1	1	0.1	0.1	0.5	0.1		0.1	0.5	0.1	0.1		0.1	0.1	0.1	0.5	0.5	0.1	10	1	8			1	0.5	0.1	0.5	2	2	5	5	5	5	3	0.5	1	1	8	10	8	4	2	4		
Festuca altissima	1.1														0.1																		1		3	1	0.1	0.1												
Festuca gigantea	1.1																																										0.5							
Fraxinus excelsior	2.1	1	0.1	1		0.5		0.5	0.5	0.5	0.5	0.5	2	3	0.5	0.5	1	0.5	0.5	3	3	1	0.5	0.5		1	1		1	0.5	1	0.1	0.5						1	0.1	2	0.5	4	5	4	2	1	5	8	1
Galeopsis tetrahit	2.1																					0.1																		0.1										
Galium odoratum	1.1	4	0.5		0.5	0.5	3	0.5	6	2	3	0.1	1	0.5	2	0.5	4	5	0.5	2				3	0.5		0.5						2	2	2		1	0.5			1			0.5	0.5	2	2	0.5	1	0.5
Geranium robertianum	2.1																																							0.1			0.5							
Geum urbanum	2.1								0.1		0.1											0.1				2																				2	0.5			0.1
Glechoma hederacea	2.1																									3																				0.5	1		0.5	
Hedera helix	1.1	0.1	0.1	0.1	0.5		0.5	0.1				0.1			0.1	0.1		0.1	2	2					4	1		0.1	0.1		2				1	0.5										1	2			
Ilex aquifolium	1.1																					0.1																				10								
Impatiens noli-tangere	1.1																																						0.1				2	1						
Impatiens parviflora	1.1																																									1	0.1							
Juncus effusus	2.1																																			3										0.1	0.1			
Lamium galeobdolon	1.1	3	0.5	0.1		1	0.5	0.5	13	20	12	2	1	3	0.1	0.5		1	0.1	0.5						6	0.5	15	8	8	2			0.1							0.5	0.5				0.5	3	2	0.5	6	0.5
Larix decidua	1.1																					0.1																											
Lonicera periclymemum	2.1																								0.1					0.1																				
Lonicera xylosteum	1.1						0.5								0.5				0.1			0.1																			0.1									
Luzula pilosa	1.1																	0.1		0.1																					0.1									
Maianthemum bifolium	1.1																								0.1	0.5																								
Malus sylvestris	1.1																																								0.1									0.1
Melica uniflora	1.1		0.5		0.5		0.5			0.5			0.5		0.5	0.5		0.5	0.5	0.5	1	0.5	3		2		1	0.1	1	0.1	0.5	1		0.1	0.5	0.1	1	0.5	0.5	0.5	1	2	8	2	0.5	4	2
Milium effusum	1.1	0.5			0.1	0.1	1	0.1	0.1	0.5	0.1	0.1	0.5	0.1	0.5	1	0.5	0.5	0.5	0.5			0.1	0.5	0.1	0.5	0.1	0.5	0.1	0.5	0.1	1		0.1	0.5	0.1			0.5	0.5	0.5	0.5	0.5	4	0.1	0.5	0.5
Oxalis acetosella	1.1	0.5	0.1				0.5	0.5	0.5	2	0.5	0.5	0.1	0.5				0.5	0.1	0.5	1	2	0.1		0.1	1		0.5	0.1										0.1		0.5	0.5	0.5	0.5						
Paris quadrifolia	1.1																																														0.1			
Poa nemoralis	1.1	0.1					0.1	0.5						0.1																																				
Poa trivialis	2.1						0.1				0.1		0.5	0.5	0.5	0.1									1																									
Polygonatum multiflorum	1.1		0.1	0.1		0.1	0.5								0.1							0.1			0.5	0.1							0.1								0.1	0.1	0.1		0.1		0.1	0.1	0.1	1
Primula elatior	1.1		0.1									0.1														0.1																					0.1			0.1
Prunus avium	2.1	0.1							0.1			0.1	0.1	0.1																0.1															0.1	0.5	0.1	0.1	0.1	
Prunus padus	2.1																														0.5																			0.5
Pteridium aquilinum	1.1																																					5												
Pulmonaria officinalis	1.1													0.1												0.5																							
Quercus robur	2.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1			0.1						0.1		0.5	0.1	0.5			0.5	0.5		0.1	0.1	0.1				0.1	0.1	0.5			0.1						
Rubus caesius	2.1																											2																						
Rubus idaeus	1.2			0.1							0.1											1				0.5				0.5		3			4				0.5	0.1		0.1			0.5	0.5	2	8	1	0.5	0.5
Rumex sanguineus	1.1																																								0.1									
Sorbus aucuparia	2.1						0.1																																						0.1	0.1				
Stachys sylvatica	1.1																	0.5																									1				1		0.1	
Stellaria holostea	1.1		0.1	2	0.5	0.5	10		4	5	10	2	3	0.5	0.5	0.5		0.1	0.5	0.1		0.5			0.5	1			0.5			1			0.1	0.1	0.5	1		1			0.1	0.5	1	1
Stellaria nemorum	1.1																										1					1			2							2	0.5	1		1		1	2
Ulmus glabra	1.1																								0.5										0.5	0.1					0.5								
Urtica dioica	2.1																									0.5	0.1					0.1								0.1					2	2	0.5	0.1	1
Veronica montana	1.1	0.1						0.5	0.5			0.1	0.1		0.1						4												2							1		1		
Viola reichenbachiana	1.1	0.1			0.1	0.5		0.5	2	0.5		0.1	1		0.1		0.1	0.1								1									0.1						0.5					0.1			0.1	0.1