Separating forest continuity from tree age effects on plant diversity in the ground and epiphyte vegetation of a Central European mountain spruce forest

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ABSTRACT

Forest continuity has been identified as an important factor influencing the structure and diversity of forest vegetation. Primary forests with centuries of continuity are usually more diverse than young secondary forests as forest are colonized only slowly and because the former are richer in old tree individuals. In the present study, performed in unmanaged high-elevation spruce forests of the Harz Mountains, Germany, we had the unique opportunity to separate the effects of forest continuity and tree age on plant diversity. We compared an old-growth spruce forest with century-long habitat continuity with an adjacent secondary spruce forest, which had naturally established on a former bog after 1796 when peat exploitation halted. Comparative analysis of the ground and epiphyte vegetation showed that the plant diversity of the old-growth forest was not higher than that of the secondary forest with a similar tree age of >200 years. Our results suggest that a period of >200 years was sufficient for the secondary forest to be colonized by the whole regional species pool of herbaceous and cryptogam forest plants and epiphytes. Therefore, it is likely that habitat structure, including the presence of old and decaying trees, was more important for determining plant diversity than the independent effect of forest continuity. Our results are probably not transferrable to spruce forests younger than 200 years and highly fragmented woodlands with long distances between new stands and old-growth forests that serve as diaspore sources. In addition, our results might be not transferable to remote areas without notable air pollution, as the epiphyte vegetation of the study area was influenced by SO_2 pollution in the second half of the 20th century.

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Introduction

The distribution and abundance of forest plants is strongly influenced by forest age and stand history (Peterken and Game, 1984). Many forest species of vascular plants, lichens and bryophytes are assumed to be restricted to forests with a habitat continuity of at least several centuries (Brunet, 1993; Edwards, 1986; Peterken and Game, 1981; Rose, 1976). The same is true for invertebrates, fungi and other organism groups (Alexander, 1998; Bredesen et al., 1997; Nilsson et al., 1995). The main cause of these restrictions is the limited dispersal ability of many forest species (Hilmo and Såstad, 2001; Sillett et al., 2000; Verheyen et al., 2003). Therefore, such species are bound to (primary) old-growth forests or at least ancient secondary forests with long habitat continuity. Managed forests with repeatedly interrupted habitat continuity lack many species of old-growth forests (Gustaffson and Hallingbäck, 1988; Kuusinen and Siitonen, 1998). Young, small forest patches in fragmented landscapes can even be largely devoid of typical forest species (Dzwonko and Loster, 1988).

In Central Europe, where humans began to interrupt the continuity of forest cover with the import of agriculture from the Middle East as early as in the Neolithic (Haak et al., 2010; Pichler et al., 2011), completely undisturbed forests are lacking. However, a few primeval forest patches still exist where stand history can be traced back for many centuries and at the same time, stand structure suggests that these forests have likely never experienced stand-level disturbance by humans (Ellenberg and Leuschner, 2010). Such primeval forests are today often located in conservation areas, whereas most forest stands with interrupted habitat continuity are managed and, thus, lack over-mature and decaying trees. Therefore, it is often difficult to separate the effect of forest continuity on species diversity from the effect of tree age.

Though many species have been classified as to be characteristic of ancient forests in the sense of long habitat continuity in expert assessments (e.g. Rose, 1976; Wulff, 1997), such studies do not distinguish between species whose reproduction biology restricts them to forests with uninterrupted or, at least, long-term continuity (Grashof-Bokdam and Geertsema, 1998; Hilmo et al., 2011) and species with a preference for site conditions which are mainly

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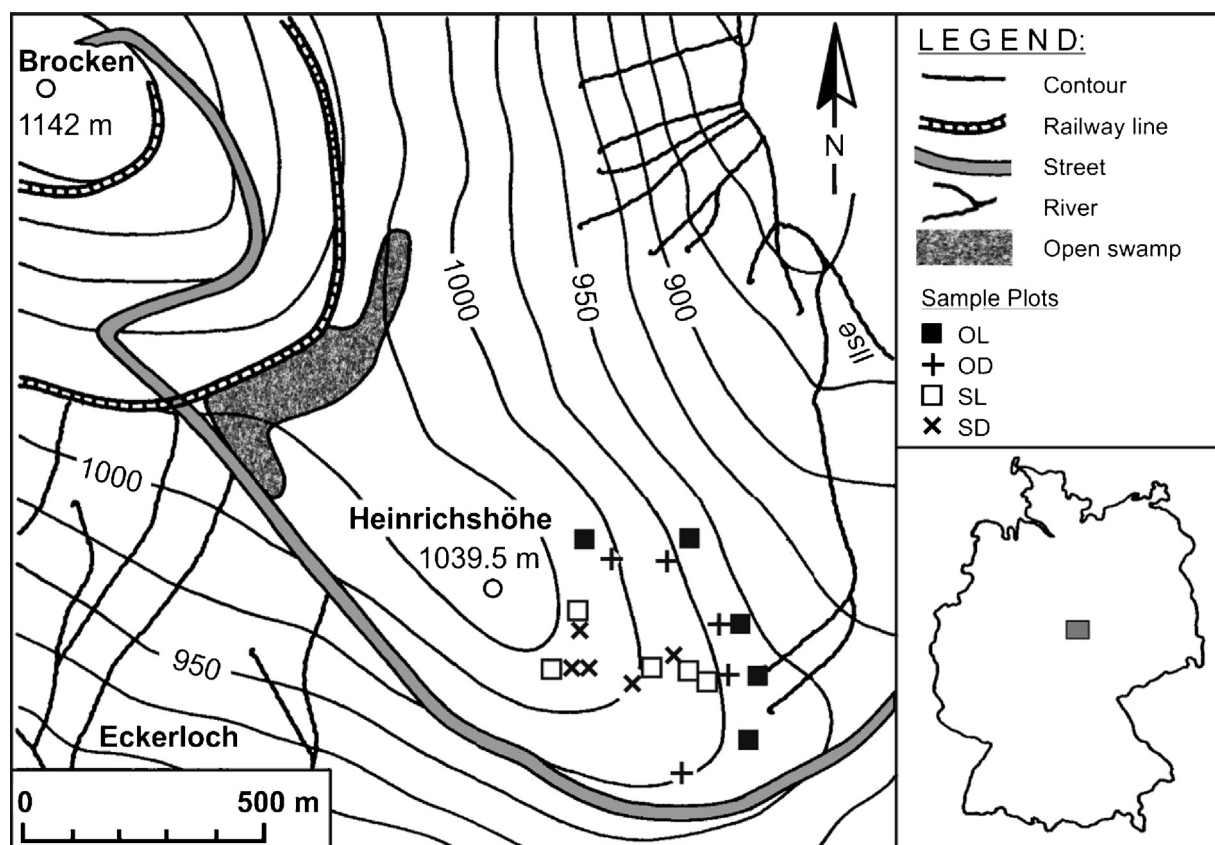 E-mail address: mhauck@gwdg.de (M. Hauck).

Fig. 1. Location of the study area within Germany and location of the sample plots (old growth forest, live [OL] and dead trees [OD]; secondary forest, live [SL] and dead trees [SD]) on Mt. Brocken.

found in forests with old tree individuals (Hauck, 2011; McGee and Kimmerer, 2002; Moning et al., 2009). The greater importance of substrate specificity and habitat persistence over continuity in forest cover and dispersal limitations has been discussed for species in boreal forests (Gibb et al., 2006; Lõhmus and Lõhmus, 2011; Nordén and Appelqvist, 2001). In Central Europe, options for the comparative study of forests with old trees with or without interrupted continuity are naturally limited because of the scarcity of unmanaged forest stands with different continuity. Comparative approaches partly include forests with contrasting site conditions and different tree species composition, which limits conclusions (Kühn, 2000).

In the present study, we had the unique opportunity to directly compare two montane stands of Norway spruce (*Picea abies* (L.) H. Karst.) with contrasting history. Both stands were comprised of more than 200-year old trees, but strongly differed in the duration of forest cover. One stand is an old-growth forest, which had been banned for logging since the early Middle Ages. The other stand developed through natural succession on an exploited and drained bog at the end of the 18th century and was, like the old-growth forest, never logged afterwards and, thus, has a cohort structure. Both the old-growth forest and the secondary forest share old trees with an age far beyond the rotation age in managed forests. However, these stands strongly differ in the continuity of their existence. We used this setting for an attempt to separate the effect of forest age (or continuity) on plant diversity from that of tree age. Our study covered the ground vegetation as well as epiphytic lichens and bryophytes on live and dead trees. The aim of the study was to test the hypothesis that both ground vegetation and epiphyte vegetation are more diverse in the old-growth (primary) forest than in the secondary forest despite similar tree age.

Materials and methods

Study sites

The study was conducted in a forest of Norway spruce (*Picea abies* (L.) H. Karst.) in the Harz National Park on Mt. Brocken in Germany (51°47′ N, 10°38′ E, Fig. 1). Our investigations were carried out on the eastern and south-eastern slopes of Mt. Brocken between 950 and 1025 m a.s.l. The regional climate is characterized by high annual precipitation of 1600 mm (including annual snowfall of 1.9 m) and a mean annual temperature of 2.9 °C (Glässer, 1994). The local bed rock is iron-rich granite, creating strongly acidic soils. Dominant soil types (FAO, 2006) include cambisol and stagnogley, depending on the groundwater level. The predominant humus form is more-like mold.

The old-growth (putatively primary) spruce forest ('Brockenurwald', 300 ha) had been banned for logging and forest pasture, as it was part of a hunting ground for nobility and clergy since the time of Charles the Great (ca. 800 AD; Jacobs, 1870; Schade, 1926). This way of protection lasted until the High Middle Ages; from the plague pandemic in the mid 14th century until the early 16th century the Harz Mountains had a very low population density. Documents and charcoal remnants give evidence of logging activities at lower elevation of Mt. Brocken, but not in the upper elevations of our study sites because of bad accessibility (Greger, 1992; Kortzfleisch, 2008). Since the introduction of systematic forest management in the late 17th century, the forest was never subjected to timber harvest (Bei der Wieden and Böckmann, 2010). Therefore, this forest is considered a forest with uninterrupted habitat continuity and is probably a primary forest. The co-occurrence of different forest age stages in a small-scale pattern of irregularly distributed patches is characteristic of this old-growth forest (Kathke and Bruelheide, 2010;

Stöcker, 2001, 2002). The oldest trees in this stand are more than 280 years old (Hauck et al., 2012a).

The nearby secondary forest has developed on a former bog site which had been exploited for peat since c. 1740 (Kortzfleisch, 2008). The extraction of peat, which was partly dug down to the bedrock (Beug et al., 1999), was finally abandoned in 1796 (Kortzfleisch, 2008). Afterwards, the drained and exploited sites were colonized by Norway spruce, creating uniform stands (Wegener and Kison, 2002), which are now more than 200 years old. Throughout the paper, we use the terms 'old-growth' and 'secondary' forests to differentiate the probably never-logged stand from the stand which has been established on the former bog in the course of secondary succession.

Sample plot selection

In both forest sites, groups of old, live trees and dead trees were selected, structurally corresponding to the over-mature and decay stages of natural spruce forest dynamics (Stöcker, 1997). Most of the dead trees had been damaged by bark beetle (*Ips typographus* L.), which is a common cause of spruce dieback in the upper Harz Mountains (Wegener et al., 2003); others are probably the remnants of the dieback from SO_2 pollution during the second half of the 20th century (Hauck et al., 2012a). Each plot type, i.e. OL (old-growth forest, dominated by live trees), OD (old-growth forest with many dead trees), SL (secondary forest, live trees) and SD (secondary forest, dead trees), was represented by five replicate sample plots of 10 m × 10 m. Random plot selection was not possible due to the limited size of the study area.

Vegetation surveys

The ground vegetation was recorded by estimating the cover of all species of vascular plants, bryophytes and lichens. For woody plants, data were recorded separately for the tree (>2 m height), shrub (<2 m) and herb layers. Ground-inhabiting bryophytes and lichens were noted as a separate cryptogam layer. Each relevé was recorded from the entire plot size of 100 m^2, which follows the range of plot sizes recommended for vegetation analyses in temperate and boreal forests (Dierschke, 1994). The cover of the individual species was estimated in percent using 5%-intervals for species covering ≥10% of the plot area and 1%-intervals for the other species. Species covering less than 1% were put to 0.5% (if more than one individual was present) or 0.1% (one individual). Epiphytic bryophytes and lichens as well as vascular plants occasionally growing on wood were recorded from the trunks of all live and standing dead trees with a minimum height of 2 m. On the studied trees, cover of all species was recorded from trunk segments including the lower 2 m above the ground and all aspects (Hauck et al., 2002). Cover was estimated in the same manner as with ground vegetation. Nomenclature of species is based on Wisskirchen and Haeupler (1998, vascular plants), Koperski et al. (2000, bryophytes) and Wirth et al. (2013, lichens).

Structural characteristics and soil properties

Some structural characteristics of the sample plots are compiled in Table 1. Within the plots, diameter at breast height (dbh) of all sample trees was measured with a diameter tape. Height of all trees with a dbh > 7 cm was measured with a Vertex IV sonic clinometer and a T3 transponder (Haglöf, Långsele, Sweden). Length and diameter of lying trunks were also measured with a measuring tape. A photograph of the canopy was taken in every plot using a hemispherical lens (Coolpix 8400 with Fisheye converter UR-E16, Nikon, Tokyo, Japan). To avoid interference with the ground vegetation, the camera was positioned at 1.0 m above the ground. The

hemispherical photos were taken on days with even overcast sky. Pixels of the photographs were assigned to gaps or areas covered by the canopy with gray scale reduction. Canopy closure is given in percent of the photographed area.

Soil samples were taken from a soil profile in the center of each plot. The pH was measured in aqueous suspension. To analyze concentrations of Ca, K, and Mg, fresh soil samples were extracted in 0.2 M BaCl$_2$ solution and measured with ICP-OES (Optima 5300 DV, Perkin Elmer, Waltham, Massachusetts, USA). Concentrations of C and N, as well as the *C/N* ratio were obtained from dry soil samples measured with a CN analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany). Results of the soil analyses revealed marked differences in the soil-properties between old-growth and secondary forests, particularly in the nutrient concentrations (Table 1).

Data analysis

Arithmetic means ± standard errors are presented throughout the paper. Statistical analyses were calculated with R 2.14.0 software (R Development Core Team, Vienna, Austria). All data were tested for normal distribution with the Shapiro–Wilk test. The significance of differences between the individual plot types was tested with the Kruskal–Wallis test, as the data were not normally distributed. The dominance structure of the vegetation was quantified by calculating N_1-diversity, which is defined as a modified Shannon function $N_1 = e^{H'}$ (Krebs, 1999); in this equation, H' is the Shannon function ($H' = -\sum p_i \ln p_i$; with p_i being the cover of species i divided by the total cover of all species in the relevé). N_1 specifies the number of equally abundant species producing the same diversity value as the calculated Shannon–Wiener function H'. Strong differences between N_1 and the total number of species (α-diversity) in a relevé illustrate the dominance of single species (i.e. the reduction of evenness). Non-metric multidimensional scaling (NMDS) calculated with Euclidean distances was applied to study differences between the individual forest development stages in variation of ground plant and epiphyte cover. In the ground vegetation, the response of individual plant species to selected soil variables (Ca, K, Mg, *C/N* ratio, pH, water content) and canopy cover was tested with canonical correspondence analysis (CCA). Both the NMDS and CCA ordinations were calculated using the program PCord 5.14 (MjM Software, Glenneden Beach, Oregon, USA). To test for significant differences in the community composition between the forest structure types, epiphyte and ground vegetation relevés were subjected to the multivariate, non-parametric analysis of similarities (ANOSIM; Clarke, 1993) using PAST 2.15 software (Ø. Hammer, Natural History Museum, University of Oslo, Norway).

Results

Ground vegetation

The ground vegetation in the old-growth forest and the secondary forest was dominated by the vascular plant species *Deschampsia flexuosa*, *Calamagrostis villosa*, *Vaccinium myrtillus* and *Galium saxatile* (Table 2). *Trientalis europaea* (and with an insignificant trend also *Oxalis acetosella*) were more abundant in the secondary forest. *Luzula sylvatica* was mainly found in the old-growth forest. The cryptogam layer in all forest types was dominated by *Plagiothecium undulatum*, *Dicranum scoparium* and *Polytrichum formosum*. The latter was most abundant in old-growth plots dominated by dead trees. The abundance of *Dicranum scoparium* was significantly higher below living than dead trees in either forest type. The mean cover of *Plagiothecium denticulatum*, *Lophocolea heterophylla*, *Amblystegium serpens* and *Tetraphis pellucida* was

Table 1
Structural characteristics and soil properties of the studied old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees). Arithmetic means ± standard error ($N = 5$), minimum and maximum values in brackets.

	OL	OD	SL	SD	P^f
Soil profile depth (cm)	51 ± 4	51 ± 2	65 ± 6	65 ± 3	*
Soil water content[a,b]	96 ± 11	129 ± 19	108 ± 12	120 ± 15	
C/N ratio[c]	19.4 ± 1.0	19.0 ± 0.9	19.3 ± 0.5	20.6 ± 0.4	
C_{total}[b,c]	28.4 ± 2.8	23.7 ± 3.4	20.9 ± 0.63	20.2 ± 2.0	
Ca[c] (mol g^{-1})	0.17 ± 0.07	0.15 ± 0.04	0.03 ± 0.00	0.02 ± 0.00	**
K[c] (mol g^{-1})	0.08 ± 0.01	0.06 ± 0.01	0.03 ± 0.00	0.03 ± 0.00	**
Mg[c] (mol g^{-1})	0.05 ± 0.01	0.05 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	**
N[c] (mol g^{-1})	0.8 ± 0.11	1.03 ± 0.13	0.68 ± 0.06	0.66 ± 0.05	
pH_{H_2O} [c]	3.6 ± 1.0	3.7 ± 0.7	3.7 ± 0.7	3.8 ± 1.0	
Canopy cover (%)	85 ± 1	74 ± 2	92 ± 1	90 ± 1	**
Living trees[d] ha^{-1}	420 ± 36	0 ± 0	400 ± 40	60 ± 36	**
dbh of living trees (cm)	47 ± 2	0 ± 0	34 ± 1	45 ± 2	**
	(20–64)	(0)	(6–60)	(28–38)	
Height of living trees (m)	21 ± 1	0 ± 0	18 ± 0	18 ± 1	**
	(9–28)	(0)	(2–26)	(15–20)	
Saplings[e] ha^{-1}	2560 ± 1024	1660 ± 598	1560 ± 395	700 ± 265	*
Dead trees[d] ha^{-1}	140 ± 46	360 ± 36	160 ± 46	1120 ± 131	**
dbh of dead trees (cm)	22 ± 6	50 ± 5	21 ± 1	22 ± 2	*
	(9–56)	(6–71)	(10–31)	(3–47)	
Height of dead trees (m)	7 ± 1	14 ± 3	7 ± 0	5 ± 0	
	(3–18)	(2–26)	(2–7)	(2–22)	

[a] Soil depth 0–60 cm.
[b] % of dry weight.
[c] Soil depth 0–20 cm.
[d] Spruce trees ≥ 2.0 m.
[e] Spruce trees <2.0 m.
[f] Levels of significance *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ (Kruskal–Wallis test).

Table 2
Cover (in %; arithmetic means ± standard error, $N = 5$) of vascular plant, bryophyte and lichen species occurring in the ground vegetation of the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees).

	OL	OD	SL	SD	P^b
Cover herb layer	71 ± 2	74 ± 3	70 ± 3	78 ± 3	
Cover cryptogam layer	46 ± 8	38 ± 7	55 ± 5	45 ± 6	
Herb layer[a]					
Deschampsia flexuosa	46 ± 11	28 ± 11	42 ± 7	32 ± 6	
Calamagrostis villosa	20 ± 6	41 ± 8	19 ± 6	53 ± 10	
Vaccinium myrtillus	17 ± 5	9.0 ± 5.8	12 ± 4	4.6 ± 1.2	
Galium saxatile	5.4 ± 2.7	12.3 ± 3.4	3.8 ± 1.0	7.4 ± 3.0	
Luzula sylvatica	3.1 ± 2.7	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	
Oxalis acetosella	1.1 ± 0.4	1.0 ± 0.2	10.8 ± 4.5	3.4 ± 1.7	
Picea abies	0.7 ± 0.2	0.5 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	
Dryopteris dilatata	0.4 ± 0.2	0.6 ± 0.2	1.0 ± 0.2	0.9 ± 0.1	
Trientalis europaea	0.4 ± 0.2	0.5 ± 0.1	2.3 ± 0.7	3.6 ± 0.7	**
Sorbus aucuparia	0.1 ± 0.1	<0.1	0.4 ± 0.1	0.2 ± 0.1	
Cryptogam layer[a]					
Mosses					
Plagiothecium undulatum	27 ± 5	18 ± 2	34 ± 3	27 ± 5	
Dicranum scoparium	5.9 ± 3.2	0.7 ± 0.3	4.2 ± 0.7	1.2 ± 0.9	*
Polytrichum formosum	2.8 ± 0.8	13 ± 2	9.2 ± 1.5	9.8 ± 4.7	*
Plagiothecium laetum	2.0 ± 1.8	0.1 ± 0.1	0.6 ± 0.4	1.9 ± 1.4	
Rhytidiadelphus loreus	0.9 ± 0.3	1.3 ± 0.8	1.4 ± 0.1	0.8 ± 0.3	
Plagiothecium denticulatum	0.5 ± 0.2	0.2 ± 0.1	2.4 ± 0.7	2.1 ± 0.8	*
Sphagnum girgensohnii	5.1 ± 3.4	0.8 ± 0.5	0.6 ± 0.2	0.0 ± 0.0	
Pleurozium schreberi	0.2 ± 0.2	0.2 ± 0.1	0.0 ± 0.0	0.3 ± 0.1	
Dicranum fuscescens	0.0 ± 0.0	2.4 ± 1.7	1.8 ± 0.3	2.1 ± 0.6	
Amblystegium serpens	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2	**
Pohlia nutans	<0.1	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	
Tetraphis pellucida	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	*
Liverworts					
Barbilophozia lycopodioides	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.3 ± 0.2	
Lophocolea bidentata	<0.1	0.2 ± 0.1	$0.1 \pm <0.1$	0.2 ± 0.2	
Lophocolea heterophylla	0.0 ± 0.0	<0.1	0.2 ± 0.1	0.2 ± 0.1	*
Lepidozia reptans	0.0 ± 0.0	<0.1	<0.1	0.1 ± 0.1	
Lophozia ventricosa	<0.1	0.0 ± 0.0	<0.1	0.0 ± 0.0	
Lophozia incisa	0.0 ± 0.0	0.1 ± 0.1	<0.1	0.0 ± 0.0	

[a] Rare species (one or two structure types, ≤ 0.2% mean cover): old-growth forest: *Senecio sylvaticus*; *Brachythecium salebrosum*, *Cladonia polydactyla*, *Plagiomnium affine*, *Polytrichum commune*, *Sphagnum russowii*; *Diplophyllum albicans*. Secondary forest: *Carex canescens*, *Urtica dioica*; *Herzogiella seligeri*, *Rhytidiadelphus squarrosus*; *Barbilophozia floerkei*, *Calypogeia azurea*, *Calypogeia muelleriana*, *Cephaloziella hampeana*, *Cephalozia leucantha*, *Cephalozia lunulifolia*, *Chiloscyphos polyanthus*.
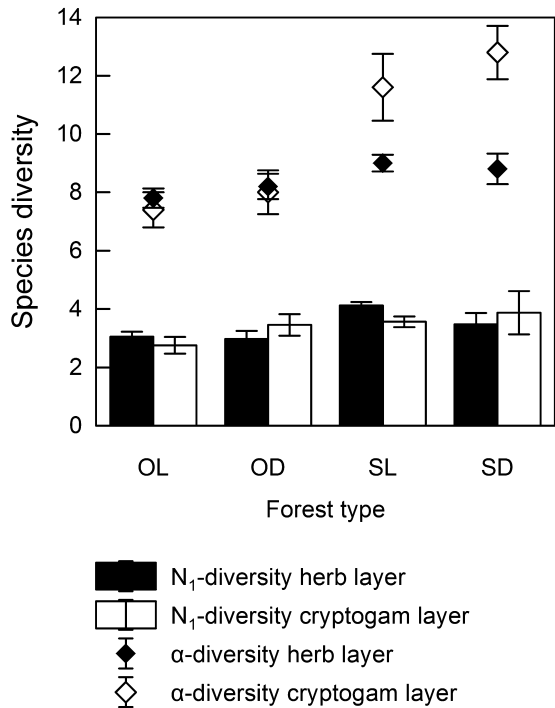[b] Levels of significance *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ (Kruskal–Wallis test).

Fig. 2. N_1- and α-diversities of ground vegetation plots in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees).

significantly higher in the secondary than in the old-growth forest. The secondary forest was richer in liverwort species than the old-growth forest, though all liverwort species only reached low cover values.

The N_1- and α-diversities of the herb layer showed little variation across the different forest structure types, with a high deviation of N_1- from α-diversity in all plot types (Fig. 2). The N_1-diversity of cryptogams did not differ between the plot types either, whereas the α-diversity of the cryptogam layer was higher in the secondary forest than in the old-growth forest; in the latter, α-diversity deviated more from N_1-diversity than in the former. Moss and especially liverwort α-diversity were higher in the ground vegetation of the secondary than the old-growth forest ($P < 0.05$), whereas there was no such difference for the vascular plants (Fig. 3a). The different forest types did not form clearly differentiated clusters in the NMDS; nevertheless live trees of either site had a trend for low axis 1 scores, whereas dead trees clustered preferentially at high scores along axis 1 (Fig. 4a). In the CCA, Monte Carlo test results on the response of forest ground species to canopy cover and soil variables proved no significance of the measured site factors to species distribution. In the ANOSIM, no significant differences were found between the forest types, except between old-growth plots with dead trees and secondary plots with live trees (Table 4).

Epiphytes

The most abundant epiphytes across all plot types included the lichens *Cladonia digitata*, *C. polydactyla*, *Lepraria jackii* as well as the bryophytes *Plagiothecium denticulatum* and *Dicranum fuscescens* (Table 3). The lichen *Pseudevernia furfuracea* as well as the bryophytes *Polytrichum formosum* and *Pohlia nutans* were more frequent in the old-growth forest than in the secondary forest. *Cladonia ramulosa* was restricted to dead trees in the old-growth forest. Differences in the frequency and abundance of *Cladonia pyxidata* s.l., *Violella fucata*, *Bryoria fuscescens*, *Lepidozia reptans* and *Lophozia ventricosa* between plots dominated by living and dead trees were more pronounced in the old-growth than the sec-
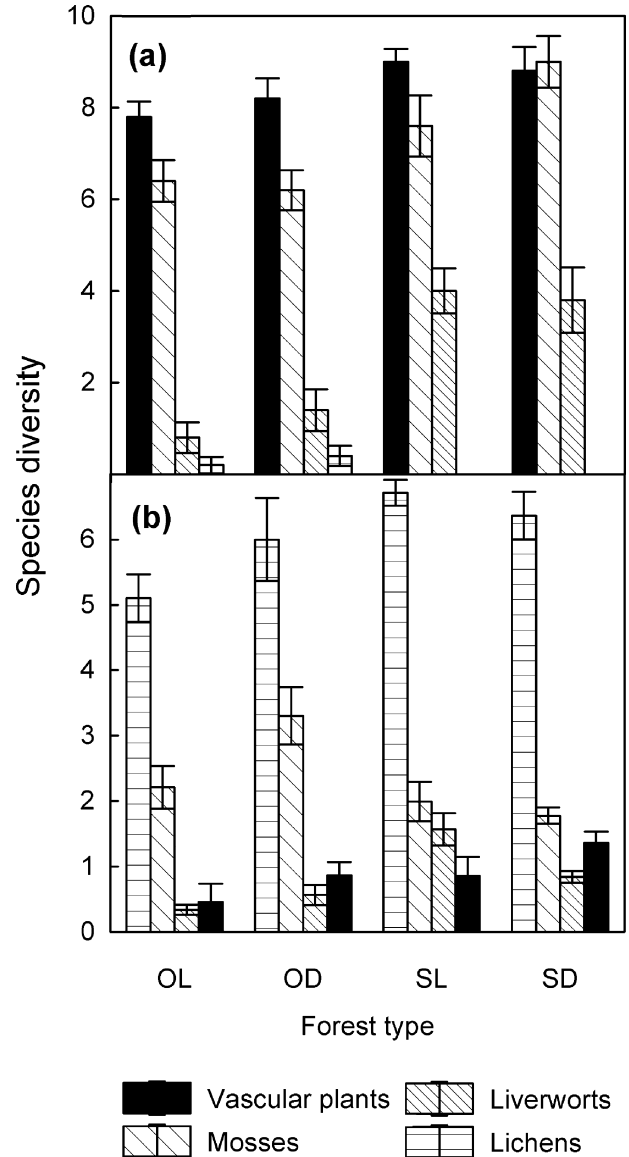

Fig. 3. Species richness (α-diversity) of different species groups in (a) the ground vegetation, (b) the epiphyte assemblages in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees).

ondary forest. Like the ground vegetation, epiphyte vegetation in the secondary forest included more liverwort species than in the old-growth forest. Among the epiphytic occurrences of vascular plants, *Vaccinium myrtillus* was most frequent across the forest types. *Trientalis europaea* and *Calamagrostis villosa* were significantly more frequent in the secondary than the old-growth forest.

The N_1-diversity of epiphytes showed little variation between the forest types, whereas the α-diversity of epiphytes was lower on live trees of the old-growth stand than in the other plot types (Fig. 5). The α-diversity of liverworts and vascular plants was higher in the secondary than the old-growth forest, whereas it was the other way round for mosses (Fig. 3b). The species richness of lichens was largely independent of the forest type. In the NMDS, no separate clusters were found for different forest types (Fig. 4b). The ANOSIM was more sensitive and revealed differences between the live trees of the secondary forest and the trees in the old-growth forest as well as between live and dead trees of the old-growth plots (Table 4).

Table 3
Frequency (in % of trees, arithmetic mean of plot-wise mean values) and cover (in %; arithmetic means ± standard error) of trunk-inhabiting epiphytes growing at 0–2 m height above the soil level on trees of a minimum height of 2 m in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees) ($N = 5$).

	OL		OD		SL		SD		p^b
Total cover		26 ± 5		37 ± 6		20 ± 3		26 ± 6	
Lichens[a]									
Cladonia digitata	93	5.8 ± 1.1	95	7.8 ± 0.8	73	2.2 ± 0.6	75	5.5 ± 1.3	**
Lepraria jackii	92	5.8 ± 1.8	87	9.1 ± 2.7	95	7.7 ± 2.7	88	11.1 ± 4.8	
Cladonia polydactyla	91	7.0 ± 1.1	95	11 ± 3	80	4.3 ± 1.1	76	2.7 ± 0.9	
Lecanora conizaeoides	79	0.7 ± 0.2	26	<0.1	64	0.5 ± <0.1	48	0.3 ± 0.1	
Hypogymnia physodes	60	0.5 ± 0.2	57	1.2 ± 0.4	72	0.4 ± 0.1	60	1.1 ± 0.2	
Hypocenomyce scalaris	51	3.5 ± 1.3	63	3.6 ± 1.8	77	0.8 ± 0.2	70	2.0 ± 1.2	
Parmeliopsis ambigua	28	0.3 ± 0.1	58	0.3 ± 0.1	71	0.2 ± <0.1	59	0.2 ± 0.1	
Pseudevernia furfuracea	7	<0.1	18	0.2 ± 0.1	<0.1		7	<0.1	
Violella fucata	6	<0.1	22	<0.1	27	0.1 ± <0.1	55	0.3 ± 0.1	*
Platismatia glauca	0	0.0 ± 0.0	50	0.6 ± 0.2	14	<0.1	17	0.1 ± 0.1	
Cladonia ramulosa	0	0.0 ± 0.0	29	0.1 ± <0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	*
Cladonia pyxidata s.l.	0	0.0 ± 0.0	24	0.3 ± 0.2	37	0.5 ± 0.1	30	0.4 ± 0.2	*
Bryoria fuscescens	0	0.0 ± 0.0	7	<0.1	5	<0.1	3	<0.1	
Mosses[a]									
Plagiothecium denticulatum	66	0.6 ± 0.2	76	0.8 ± 0.3	39	0.2 ± <0.1	18	0.3 ± 0.1	**
Dicranum fuscescens	56	1.5 ± 0.8	78	2.4 ± 0.7	71	1.2 ± 0.9	49	0.4 ± 0.1	
Tetraphis pellucida	41	0.7 ± 0.2	61	0.8 ± 0.3	59	0.2 ± 0.1	33	0.2 ± 0.1	
Polytrichum formosum	35	0.6 ± 0.4	44	0.3 ± 0.1	17	0.1 ± 0.1	13	0.1 ± <0.1	*
Pohlia nutans	6	0.1 ± <0.1	12	<0.1	0	0.0 ± 0.0	0	0.0 ± 0.0	*
Amblystegium serpens	5	<0.1	5	<0.1	0	0.0 ± 0.0	2	<0.1	
Plagiothecium undulatum	3	<0.1	4	<0.1	13	<0.1	5	<0.1	
Brachythecium salebrosum	0	0.0 ± 0.0	17	0.4 ± 0.2	0	0.0 ± 0.0	0	<0.1	
Liverworts[a]									
Lepidozia reptans	19	0.1 ± <0.1	5	<0.1	37	0.3 ± 0.1	18	0.1 ± <0.1	
Lophocolea heterophylla	9	<0.1	10	<0.1	37	0.1 ± <0.1	14	<0.1	
Cephalozia lunulifolia	2	<0.1	5	<0.1	23	0.1 ± 0.1	3	<0.1	
Lophozia ventricosa	0	0.0 ± 0.0	22	0.1 ± 0.1	8	0.1 ± <0.1	2	<0.1	
Ptilidium ciliare	3	<0.1	0	0.0 ± 0.0	5	<0.1	6	0.1 ± <0.1	*
Lophocolea bidentata	0	0.0 ± 0.0	9	<0.1	6	<0.1	4	<0.1	
Ptilidium pulcherrimum	0	0.0 ± 0.0	5	<0.1	3	<0.1	1	<0.1	
Cephalozia leucantha	0	0.0 ± 0.0	0	0.0 ± 0.0	16	<0.1	11	<0.1	**
Vascular plants[a]									
Vaccinium myrtillus	16	0.1 ± 0.1	30	0.3 ± 0.1	22	0.4 ± 0.2	32	0.1 ± 0.1	
Deschampsia flexuosa	13	0.1 ± 0.1	17	0.1 ± 0.1	25	<0.1	16	<0.1	
Oxalis acetosella	12	<0.1	22	0.2 ± 0.1	29	<0.1	32	<0.1	
Picea abies	6	<0.1	7	0.1 ± 0.1	0	0.0 ± 0.0	2	<0.1	
Dryopteris dilatata	2	<0.1	0	0.0 ± 0.0	7	<0.1	8	<0.1	
Galium saxatile	0	0.0 ± 0.0	7	<0.1	5	<0.1	2	<0.1	
Calamagrostis villosa	0	0.0 ± 0.0	5	0.1 ± <0.1	3	<0.1	19	<0.1	*
Trientalis europaea	0	0.0 ± 0.0	0	0.0 ± 0.0	12	<0.1	25	0.1 ± <0.1	**

[a] Rare species (one or two structure types, <10% frequency): Old-growth forest: *Trapeliopsis flexuosa*; *Plagiothecium laetum*. Secondary forest: *Cladonia coniocraea*, *Lecanora filamentosa*, *Lecanora saligna*, *Mycoblastus sanguinarius*, *Parmelia saxatilis*, *Parmeliopsis hyperopta*, *Strangospora* spec., *Trapeliopsis flexuosa*; *Barbilophozia lycopodioides*, *Calypogeia azurea*, *C. muelleriana*, *Cephaloziella hampeana*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Mylia taylorii*, *Orthodicranum montanum*, *Orthotrichum* spec.

[b] Kruskal–Wallis test results for differences in cover: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Discussion

In contrast to our expectations, plant diversity in the old-growth forest was not higher than in the adjacent secondary forest, although the latter had newly established on a former bog, i.e. represents the first forest generation on non-forest soil. This applied to all studied components of the vegetation, namely the vascular plants and cryptogams on the ground as well as epiphytes on live trees and standing deadwood. This result suggests that in the case of the studied spruce mountain forest ecosystem, a period of 215 years was sufficient for vascular plants, bryophytes and lichens to colonize the newly established stand. The contrasting history of the two neighboring stands with more than up to 200-year old trees, with the one stand being an old-growth forest with long-standing habitat continuity and the other stand being successional to a non-forest ecosystem, can be assumed to be a quite unique setting in Central Europe. Tree age in both forests is far beyond the rotation age of managed spruce forests (Hilmo et al., 2009; Moog and Borchert, 2001).

Since the old-growth stand exhibited no higher plant diversity than the secondary forest, the conclusion can be drawn that forest continuity beyond a time span of 200 years is not determinative for the present composition of the ground and epiphyte vegetation in the studied mountain spruce forest. The uniqueness of the situation in the studied spruce stands unfortunately implies that no replicate sampling on the stand or the landscape levels was feasible. Therefore, the question arises to which extent the results from our case study from the Harz Mountains National Park can be generalized.

Table 4
P values resulting from ANOSIM analyzing the differences in the ground and epiphyte vegetation between the studied old-growth (OL, live trees; OD, dead trees) and secondary forest plots (SL, live trees; SD, dead trees).

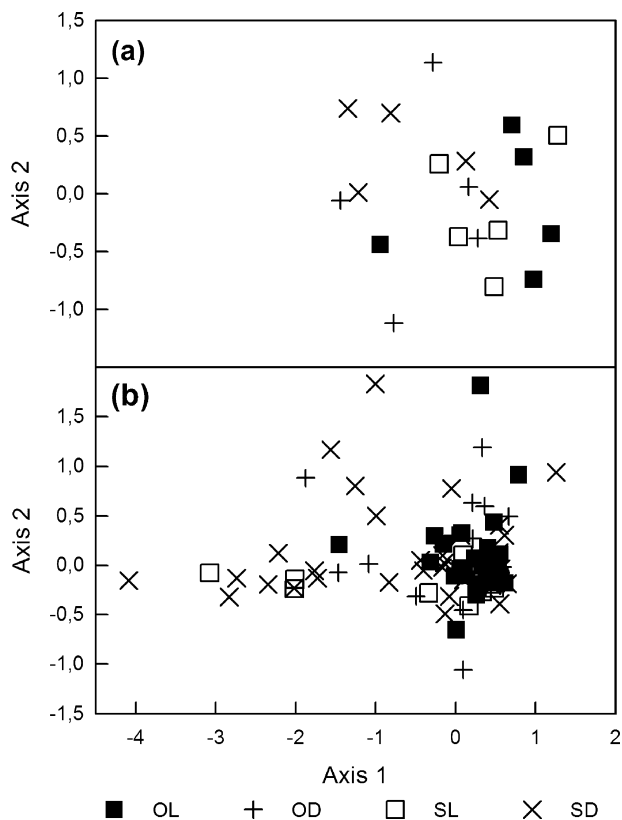|	OL	OD	SL
Ground vegetation			
OD	0.17		
SL	0.12	<0.001	
SD	0.06	0.60	0.07
Epiphytes on trees			
OD	0.02		
SL	<0.001	<0.001	
SD	0.73	0.76	0.58

Fig. 4. NMDS ordination of vegetation relevés in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees): (a) ground vegetation ($N = 20$ plots; final stress 9.89); (b) epiphytes on trees ≥ 2.0 m ($N = 133$ trees; final stress: 10.48).
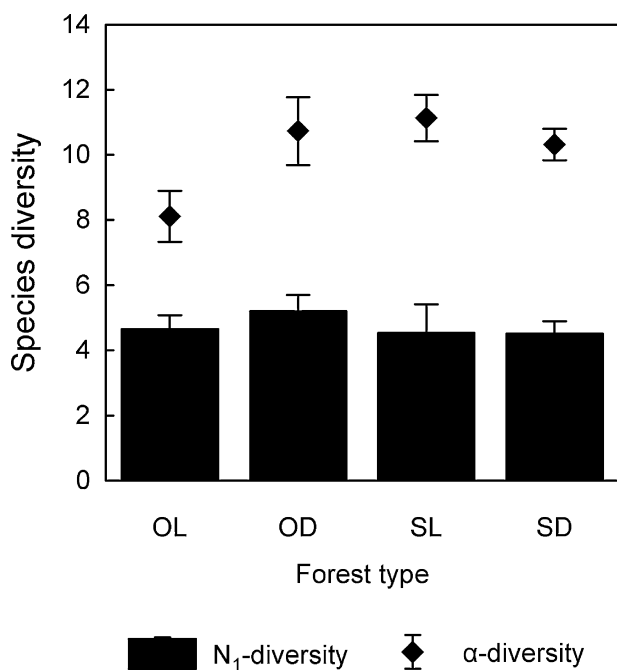

Fig. 5. N_1- and α-diversities of epiphyte vegetation in the old-growth forest (OL, live trees; OD, dead trees) and the secondary forest (SL, live trees; SD, dead trees).

A key factor that most likely has promoted the colonization of the newly established forest since 1796 is the proximity to the old growth stand. It has been substantiated repeatedly in the published literature that short distance to the next old forest is beneficial for the colonization of newly afforested sites. Such examples have been found both for the ground vegetation (Bossuyt et al., 1999; Brunet and von Oheimb, 1998; Singleton et al., 2001) and cryptogamic epiphytes (Buckley, 2011). Dispersal limitations of many forest species are the main cause behind this relationship (Hilmo and Såstad, 2001; Takahashi and Kamitani, 2004). Species saturation during the recolonization of new forest sites varies between regions and ecosystems. While many forest plants can colonize nearby newly afforested sites within 100 years (Brunet et al., 2000; Norris, 1987), other species need several centuries, as, for instance, shown for liverworts in boreal *Picea mariana* forests, where the maximum species diversity was reached after 275 years (Fenton and Bergeron, 2008). Isolated forest patches within arable land or grassland-dominated landscapes do not reach the plant species diversity of old-growth forests even after several centuries (Nagaike, 2012; Rose, 1976).

Though the studied old-growth forest has probably never been harvested, it was not exempted from any human impact. During the second half of the 20th century, the upper Harz Mountains were, like many high elevation forests in Central and Eastern Europe, exposed to high atmospheric loads of SO_2 (Hauck et al., 2012a). The SO_2 pollution was shown to have strongly influenced the epiphytic lichen vegetation in the Harz Mountains (Hauck and Runge, 1999; Hauck et al., 2002). After the dramatic reduction of the SO_2 emissions in Central Europe, soils and vegetation are presently recovering from the former SO_2 load and the resulting acidification (Hauck et al., 2011, 2012a). The SO_2 pollution has surely caused the extinction of some epiphytic lichens from the upper Harz Mountains (Hauck, 1996) and might also have reduced the species richness of bryophytes, but had probably little effect on the vascular plant vegetation (Winner and Bewley, 1978). Therefore, it is likely that the pool of epiphyte species was reduced compared to the preindustrial level. This clearly limits the ability to generalize our results; forest ecosystems which are undisturbed not only relating to forest management, but also with respect to air pollution might respond more sensitively to habitat continuity than the forest studied by us.

Certain site factors differing between the studied old-growth and the secondary forests had remarkably little effect on the vegetation. These differences included the lower concentrations of exchangeable K, Ca and Mg in the soil of the secondary forest on the exploited bog, than in the soil prevailing in the old-growth forest (Table 1). These observations are strongly supported by studies in boreal forests on drained bogs, where differences in nutrients were found not to be closely correlated with differences in forest ground vegetation either (Westman and Laiho, 2003). The content of C in the upper soil did not significantly differ between the old-growth and the secondary forests, indicating a convergence of the former (organic) bog soil to the natural forest mineral soil. Similar concentrations of N may be due to high atmospheric N-input in the study area (Böhlmann et al., 2005).

Furthermore, the mean tree diameter of live trees was higher in the old-growth than in the secondary forest, but did not cause higher epiphyte diversity in the former, though a correlation between tree diameter and species diversity has been substantiated in other studies both for epiphytic bryophytes and lichens (Hauck et al., 2012b; Mežaka et al., 2008). Lower canopy closure in the plots with dead trees in the old-growth forest than in the other plots, and in the secondary forest in particular, may explain some of the minor variation in the vegetation that was observed between the plot types, which was also supported by the results of the NMDS, indicating differences in the ground vegetation between

stands of live and dead trees. The lower cover of bryophyte species in the ground vegetation of plots with dead trees in the old-growth forest than in the other stand types might be attributable to relatively slight differences in microclimate resulting from variation of the canopy closure (Ma et al., 2010). These differences might also have caused the higher frequency of liverworts *Cephalozia leucantha* and *Ptilidium ciliare* on tree trunks of the secondary forest than the old-growth stand.

Though the study of managed spruce plantations was not part of the present investigation, it is well documented in the literature that they differ from both the studied old-growth and secondary forest stands by their considerably lower diversity of epiphytes (Peterken et al., 1992). Recent studies of the epiphytic lichen and bryophyte diversity in 80–140-year old spruce plantations of the Harz Mountains were published by Günzl (1999) and Hauck (2000) and showed a lower species diversity than in the more than 200-year old stands of the present study. Structural features that cause the higher diversity with increasing tree age include the increasing availability of thick-stemmed deadwood and large-diameter trees, which offer a higher diversity of microhabitats, such as deep furrows, cavities or inclined trunks (Dittrich et al., 2012; Fenton and Bergeron, 2008; Humphrey, 2005). The scarcity of such structural features in managed forests has caused the extinction of many epiphyte species in Central Europe; in broadleaved forests of north-western Germany, for example, Hauck et al. (2013) estimated that around one third of the epiphytic lichen species have become extinct since the mid 19th century. The ground vegetation is strongly influenced by light availability. The herb and cryptogam layers of the studied forests are similar to that of 200-year old selectively logged spruce stands in the Harz Mountains, whereas the understory vegetation in dense, dark plantations is much sparser (Niedersächsisches Umweltministerium, 1992; Damm, 1994).

Conclusions

More than 200 years of unmanaged development of the secondary spruce forest were sufficient to achieve the same diversity of vascular and cryptogamic plant species in the ground vegetation and of epiphytes on trees as was found in the nearby old-growth forest. Thus, we had to reject our hypothesis that forest continuity acts independently of, and additive to, tree age on diversity. This does not disprove that an independent habitat continuity effect exits on spruce stands <215 years in age. Comparison with published work from other regions suggests that our results are representative for cases where secondary forests have established in close proximity to old-growth forests. Here, the age of the tree individuals of the actual tree generation is apparently more crucial for shaping the vegetation than stand continuity across different tree generations. However, our results are not transferable to isolated secondary forests in open landscapes with long distances to relevant diaspore sources.

Acknowledgments

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