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Forest ecosystem research in Hainich National Park (Thuringia): First results on flora and vegetation in stands with contrasting tree species diversity

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Abstract

A floristic description is presented of the study sites of the Research Training Group "The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests". To investigate different aspects of plant biodiversity in Hainich National Park (Thuringia), deciduous forest stands with low, medium and high canopy tree species diversity were compared. The results of species richness and forest communities show that the research sites are characterised by a typical central European forest flora. Greater vascular plant species richness occurs with higher diversity of tree species. Six of altogether twelve research sites are assigned to the beech forest alliance (Galio odorati–Fagion), the second half belongs to the oak-hornbeam forest alliance (Carpinion betuli). Suballiances within the Galio odorati–Fagion in the study area include the Galio–Fagetum and the Hordelymo–Fagetum. All Carpinion betuli relevées are assigned to the suballiance Stellario–Carpinetum.

Key words

Hainich, species diversity, species richness, vegetation structure, forest plant species, beech forest, oak-hornbeam forest, Hordelymo–Fagetum, Stellario–Carpinetum

1. Introduction

Biodiversity has become one of the main topics of forest management since the 1992 Rio de Janeiro session of the United Nations Conference on Environment and Development Process (UNCED) and the Ministerial Conference on the Protection of Forests in Europe held in Helsinki in 1993. Biodiversity describes the variety of living organisms at different scales, including within-species diversity, between-species diversity, as well as diversity of ecosystems and diversity of the ecological processes which they sustain (GASTON & SPICER 2004). Species diversity is considered to be one of the key parameters characterising ecosystems and a key component of ecosystem functioning (HUTCHINSON 1959, SCHULZE & MOONEY 1994, LARSSON 2001, LOREAU et al. 2002, SCHERER-LORENZEN et al. 2005).

Currently, Central-European forestry is conducting a broad-scale conversion from monocultures to mixed stands. Against the background of climate change, the new management paradigm aims at increasing the overall biodiversity of forest communities, and at securing and increasing their capability of providing ecosystem goods and services (RÖHRIG et al. 2006). However, no in-depth study has yet addressed questions of the functioning of forest ecosystems with multiple tree species, i.e., relationships between biodiversity and productivity, or between biogeochemical cycles and biotic interactions (SCHERER-LORENZEN et al. 2005). In April 2005, work was initiated on the research project "The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests" (DFG Research Training Group 1086, DFG-Graduiertenkolleg 1086) in Hainich National Park (Thuringia, Germany). The Graduiertenkolleg 1086 (GK 1086) brings partners from the faculties of Forestry, Biology and Agriculture of the Georg-August-University Göttingen and the Max-Planck-Institute for Biogeochemistry Jena together. The exceptionally species-rich broadleaved forest (maximum 14 tree species per hectare) of the Hainich National Park provides the opportunity to analyse the influence of tree species diversity (species richness as well as life history traits) on overall biodiversity, ecosystem functioning and biotic interactions as well as on ecosystem services (THOMAS et al. 2005, GRADUIERTENKOLLEG 1086 2006). The focus of our subproject is the impact of tree species diversity on the structure, diversity, productivity, carbon storage and nitrogen cycling of herb-layer vegetation. Forest herb-layer species are sensitive indicators of site conditions resulting from both natural processes and human activities. Therefore they might be a useful and easy tool to evaluate biodiversity in order to characterise sustainable or ecosystem-based forest management as well as differences and changes in forest site conditions (SCHMITT 1936, SCHMIDT 1999, 2005). One of the central questions of the current study is whether higher tree species diversity is correlated with a higher diversity of herb-layer species. Contradictory evidence has emerged in other studies concerning the relationship between tree-layer and herb-layer diversity.

In this paper, we present first results on flora (species richness, alpha-diversity) and vegetation (forest communities, phytosociological classification) of the research sites of the GK 1086. The main objective is to provide base-line data and a centre of reference for the other subprojects of the GK 1086, and to describe and discuss some noteworthy diversity patterns.

2. Materials and Methods

2.1 Environment and history of the study area

The Hainich is located at the western border of the Thuringian Triassic basin within the northwestern Thuringian limestone plate (Grabietz & Fiedler 1996, Ahrns & Hofmann 1998). All of the research sites are situated about 350 m elevation in the north-eastern part of Hainich National Park close to the village Weberstedt (near to the Thiemsburg, Fig. 1) on flat plateaus above Upper Muschelkalk. The Hainich remained ice-free during the Pleistocene, and a layer of loess was deposited by wind (Greitzke & Fiedler 1996) resulting in a closed, homogeneous loess cover or loess-clay cover. Soil types are parabrown earth, parabrown earth-pseudogley, or transitions between these soil types (J. Schramm 2005).

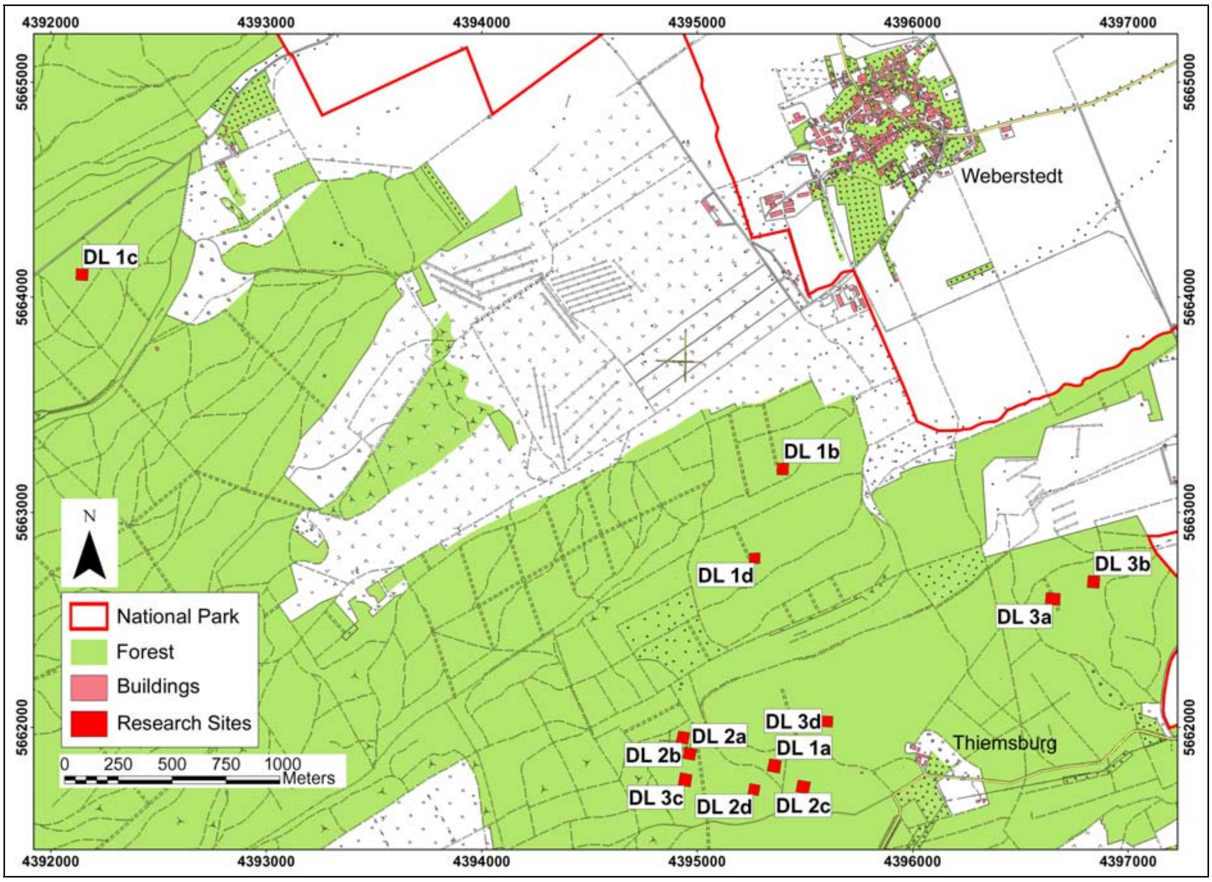

Fig. 1: Position of the research sites. DL 1: diversity level 1 plots; DL 2: diversity level 2 plots; DL 3: diversity level 3 plots; replicates indicated by letters a-d. (Map: K. M. Daenner).

The Hainich belongs to the forest growth district B.37.23 “Hainich-Dün” within the forest growth area B.37 “middle German Triassic mountain and hill country”. The climate can be characterised as subatlantic. A gradual change toward a subcontinental climate occurs toward the Thuringian basin, especially in eastern parts (Gauer & Aldinger 2005, Geiling 2005). Mean annual precipitation varies between 600 mm and 670 mm. 45 % - 50 % of the annual precipitation falls during the growing season, peaking in July. The mean annual temperature is about 7.5° C to 8.0° C (Grabietz & Fiedler 1996, Ahrns & Hofmann 1998, H. Schramm 2005, Grossmann 2006).

Despite of low impacts of early settlements, the Hainich area has seen a more intensive human use of its landscape since the 12th century. Since that time, periodic destruction and degradation of the forest likely occurred due to uncontrolled and unmitigated use. Nevertheless, compared to other parts of

Germany, harvesting of litter is of minor importance, since the farmlands in the Thuringian basin produced enough litter. Laws establishing more sustainable use were enacted in early modern times, but were largely unenforced (Mund 2004, Burse 2005). The middle of the 19th century saw a transition from the often irregular coppice with standards system (*Mittelwald*) to high forest (*Hochwald* - especially to the multiple aged forest system *Plenterwald*). The main interest behind these changes in management was that of producing larger-dimensioned timber (Fuchs at al. 1999, Mund 2004), a trend that continued until the first decades of the 20th century (Stadtverwaltung Mühlhausen 1997, Burse 2005). Due to this history, many present-day stands house very large, old trees with broad crowns and multi-stems, originating from formerly used coppices with standards systems. A dramatic change in land use occurred with military use of the southern Hainich area starting in 1935. More recently, the military training areas “Weberstedt” and “Kindel” were established in 1964, providing large off-limits areas of deciduous forest free of any harvesting. Thanks to this lengthy period of unmanaged status, and the resulting forest maturity and relative wildness, the area became national park in 1997, when military use ceased. Hainich National Park covers 7,500 hectares of the southern Hainich area and consists almost totally of species-rich deciduous woodlands. Nearly the whole national park area is state forest, surrounded by community forests and forest cooperatives (so-called “Laubgenossenschaften” - Schwartz 1991, Biehl 2005, Burse 2005, Grossmann 2006).

2.2 Experimental design, sampling and data analysis

Since currently the GK 1086 is an interdisciplinary project, the experimental design had to fulfil various requirements of different partners. For instance, a single project focussed on mycorrhiza may not be able to investigate as many plots as a project focussing on flora and forest communities. Due to this, a compromise research design established 12 sampling sites. Between summer, 2003 and January, 2005, 12 sites were chosen belonging to three different diversity levels (DL): DL 1, with *Fagus sylvatica* as major tree species; DL 2, having *Fagus sylvatica*, *Fraxinus excelsior*, *Tilia cordata* / *T. platyphyllos* as major tree species; DL 3, with *Fagus sylvatica*, *Fraxinus excelsior*, *Tilia cordata* / *T. platyphyllos*, *Carpinus betulus*, and *Acer pseudoplatanus* / *A. platanoides* as major tree species. *Quercus robur*, *Q. petraea*, *Prunus avium*, *Ulmus glabra*, *Acer campestre* or *Sorbus torminalis* can occur as minor species, in any of the DLs. Four replicates were selected for each DL, indicated by letters a to *d* (Fig. 1). Each research site had a size of 2,500 m² (50 m x 50 m; Fig. 2). Following Prodan (1968), Petraitis et al. (1989), Oliver & Larson (1990), Fabbio et al. (2006), and Hill et al. (2006) an area of this size can be regarded as being homogeneous in dynamics of tree populations and the associated vegetation. The research sites were chosen according to the following criteria: (1) flat or with only gentle slopes on eutrophic loess-covered soils with a depth of at least 60 cm (Brauns et al. 2006), (2) stands free of harvesting for at least four decades, (3) closed canopy and (4) homogeneous stand structure among all research sites. In each research site, the number and the diameter at breast height (dbh) of all trees with a dbh of at least 7 cm was recorded in spring 2005 (for more details see Guckland et al. *in preparation*).

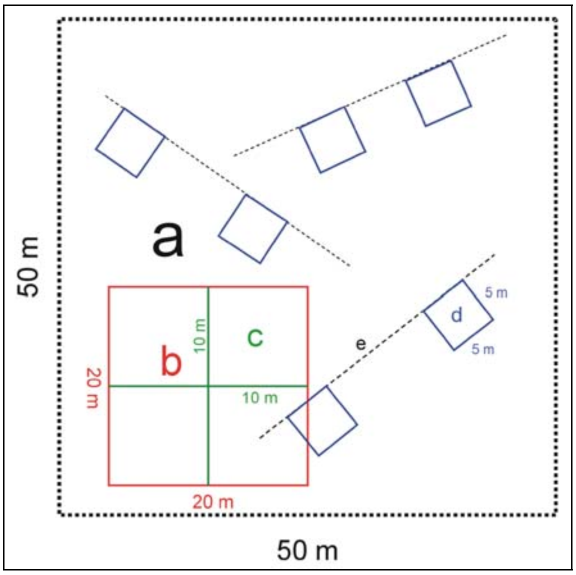

Fig. 2: Experimental design of the research sites. a: 50 x 50 m plot (2,500 m²); b: 20 x 20 m plot (400 m²); c: 10 x 10 m plot (100 m²); d: randomised 5 x 5 m plot (25 m²); e: randomised transect (length 30 m).

The units for floristic analysis and vegetation sampling were both entire research sites (2,500 m²) and the smaller plots (25 m², 100 m², 400 m²) within those sites. For comparable results with those from other European countries, a common sampling area (CSA) of 400 m² was adopted, suiting the framework of the Level II programme (ICP Forests: intensive monitoring of forest condition, SEIDLING 2005a). In the current study, 400 m² areas were represented by four plots of 10 m x 10 m (100 m²). These smaller-area sample plots allowed for more manageable size to construct relevées (EP GRVEG 2002, BOLTE & SCHULZE 2001, SEIDLING 2005a, SEIDLING 2005b). Additionally, in three of the four replicates per DL, six 25 m² plots (5 m x 5 m) were located randomly along three also randomised transects (Fig. 2). The establishment of these 25 m² plots as well as the transects also serves the research requirements of most of the other project partners in the GK 1086 (GUCKLAND et al. *in preparation*).

Due to the seasonal phenology of the herb-layer vegetation in deciduous forests, floristic inventory and vegetation sampling was done twice a year (ELLENBERG 1956, DIERSCHKE 1994): first during the flowering period of *Anemone nemorosa* (April 2005) and second during the flowering period of forest grasses, especially *Hordelymus europaeus* (July 2005). To characterise the vegetation, the sampling employed a slightly modified BRAUN-BLANQUET cover scale (rank “2” split into 2a: 5-15 % coverage, 2b: 15-25 % coverage) (DIERSCHKE 1994). The spring and summer relevées were combined by taking the higher cover value when a species was found in both relevées. Species lists for each level of diversity (DL 1, DL 2, DL 3) and sampling scale (from 25 m² up to 2,500 m²) level were prepared in order to compare species richness and species composition. Floristic similarity between diversity levels was determined using the JACCARD similarity coefficient (JACCARD 1901, DIERSCHKE 1994). To determine typical forest-dependent plant species, an assignment of each occurring species to one of the categories of the list of forest plants of hillsides and mountains in Germany (SCHMIDT et al. 2003) was done for each diversity level. The classification system of ELLENBERG (2001) was applied to the dataset to obtain a clearer view of the distribution of species that characterise different phytosociological groups. Nomenclature of vascular plants follows WISSKIRCHEN & HAEUPLER (1998), and that of bryophytes follows KOPERSKI et al. (2000).

For statistical analyses the Kruskal-Wallis-H-test ($p<0.05$) with subsequent Mann-Whitney-U-test, using SAS (© SAS Institute, Inc.) was applied. To compare tree-layer species diversity with herb-layer species diversity, tree species were removed from the herb layer data since these species are not independent from the inapt variable of “tree species diversity”.

3. Results

3.1 Flora and floristic diversity

In all sites collectively, a total of 108 vascular plant species (including 13 tree species) and 19 bottom layer bryophytes were found. 66 vascular plant species (including 10 tree species) and 4 bryophyte species were detected in DL 1, 84 vascular plant species (including 12 tree species) and 3 bryophyte species in DL 2, and 93 vascular plant species (including 12 tree species) and 18 bryophyte species in DL 3. 54 vascular plant species (50 % of the total vascular plant species) occur in all three diversity levels. 23 vascular plant species could be found in both DL 2 and 3, 5 in both DL 1 and 2 and two in both DL 1 and 3. DL 3 yielded 15 species not encountered in other DL, 3 were unique to DL 2, and 7 were unique to DL 1. Among the bryophytes, three species were encountered in all three diversity levels (16 % of the total bryophyte species). 15 bryophyte species appeared only in DL 3 and one bryophyte species solely in DL 1. No bryophyte species exclusive to DL 2 and no bryophyte species coexisting in two of the three diversity levels were found. Floristic similarity reached the highest proportion (72 %) between DL 2 and DL 3. The lowest similarity (51 %) was ascertained between DL 1 and DL 3, while a intermediate similarity value (58 %) was found between DL 1 and DL 2.

A greater number of vascular plant species (excluding tree species) with greater canopy tree species diversity is seen not only at the scale of overall species lists, but also among the research sites and plots (25 m², 100 m², 400 m², 2,500 m², Fig. 3). Within each diversity level, species richness is higher with larger area (Fig. 4). Mean vascular plant species number plotted versus area size is significantly correlated (DL 1: $r^2 = 0.83$; DL 2: $r^2 = 0.69$; DL 3: $r^2 = 0.76$) in all three diversity levels (Fig. 5). A significant correlation is also found for vascular plant species richness including tree regeneration versus canopy tree diversity (DL 1: $r^2 = 0.84$; DL 2: $r^2 = 0.68$; DL 3: $r^2 = 0.73$). By using species-area curves (ROSENZWEIG 2000, CRAWLEY & HARRAL 2001, DESMET & COWLING 2004) in the current study species numbers per hectare have been estimated by regression analyses. Within DL 1 the calculated number of plant species is 43, in DL 2, 64 species, and in DL 3, 75 plant species per hectare, respectively.

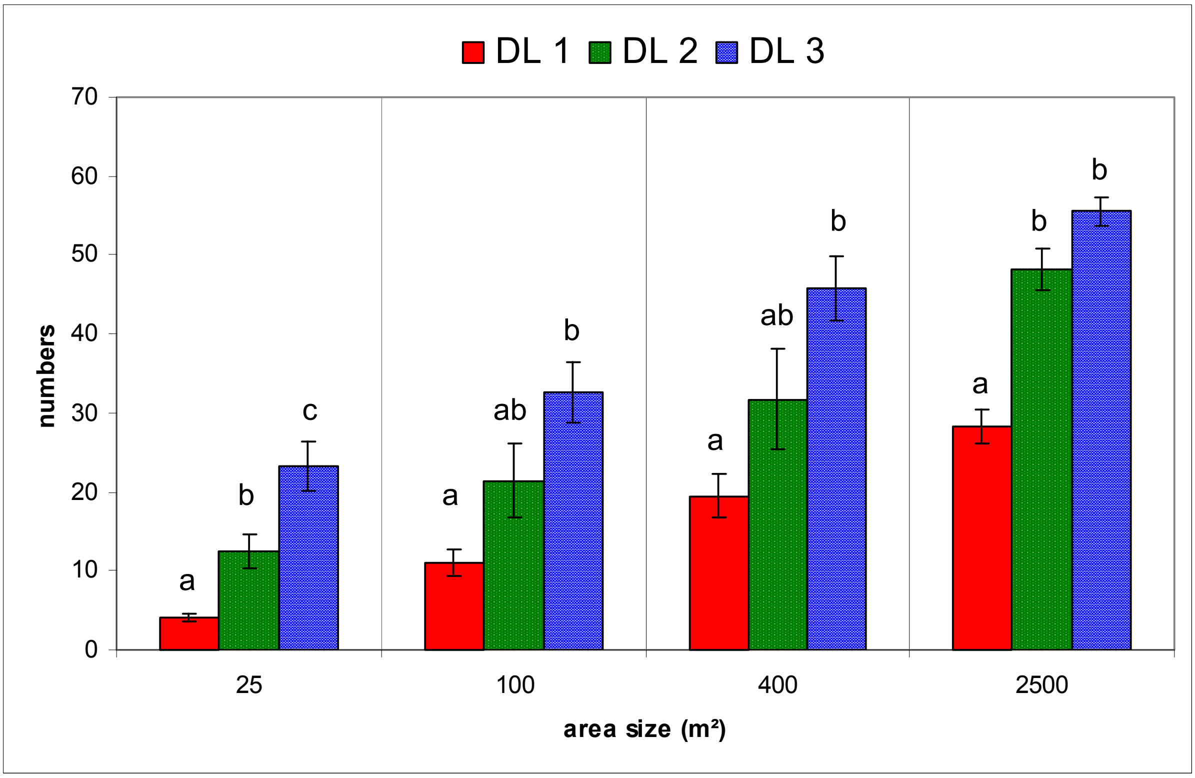

Fig. 3: Mean numbers and standard errors of vascular plant species (tree regeneration excluded) on plots of the three diversity levels DL 1, DL 2 and DL 3 for different plot sizes (25 m², N = 3; 100 m², N = 4; 400 m², N = 4 and 2,500 m², N = 4). Means that do not share the same letter differ significantly.

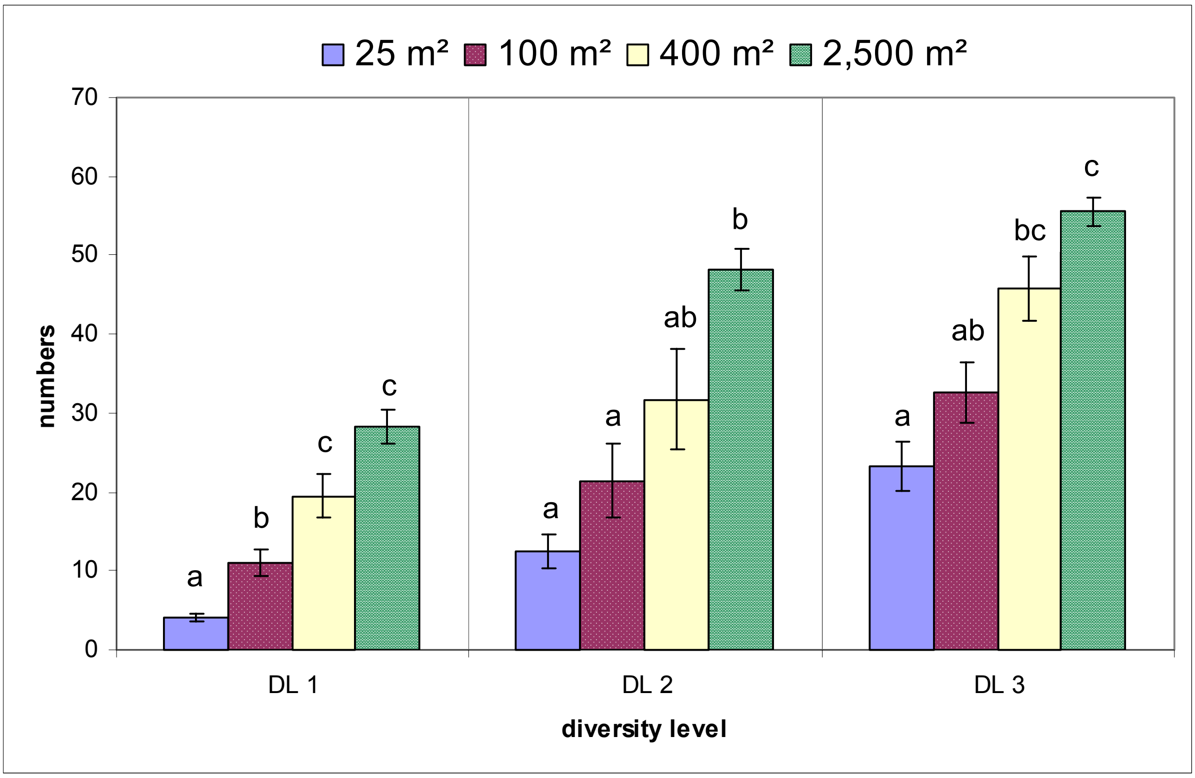

Fig. 4: Comparison of mean numbers and standard errors of vascular plant species richness (tree regeneration excluded) in plots of different size (25 m², N = 3; 100 m², N = 4; 400 m², N = 4 and 2,500 m², N = 4) grouped by the diversity levels DL 1, DL 2 and DL 3. Means that do not share the same letter differ significantly.

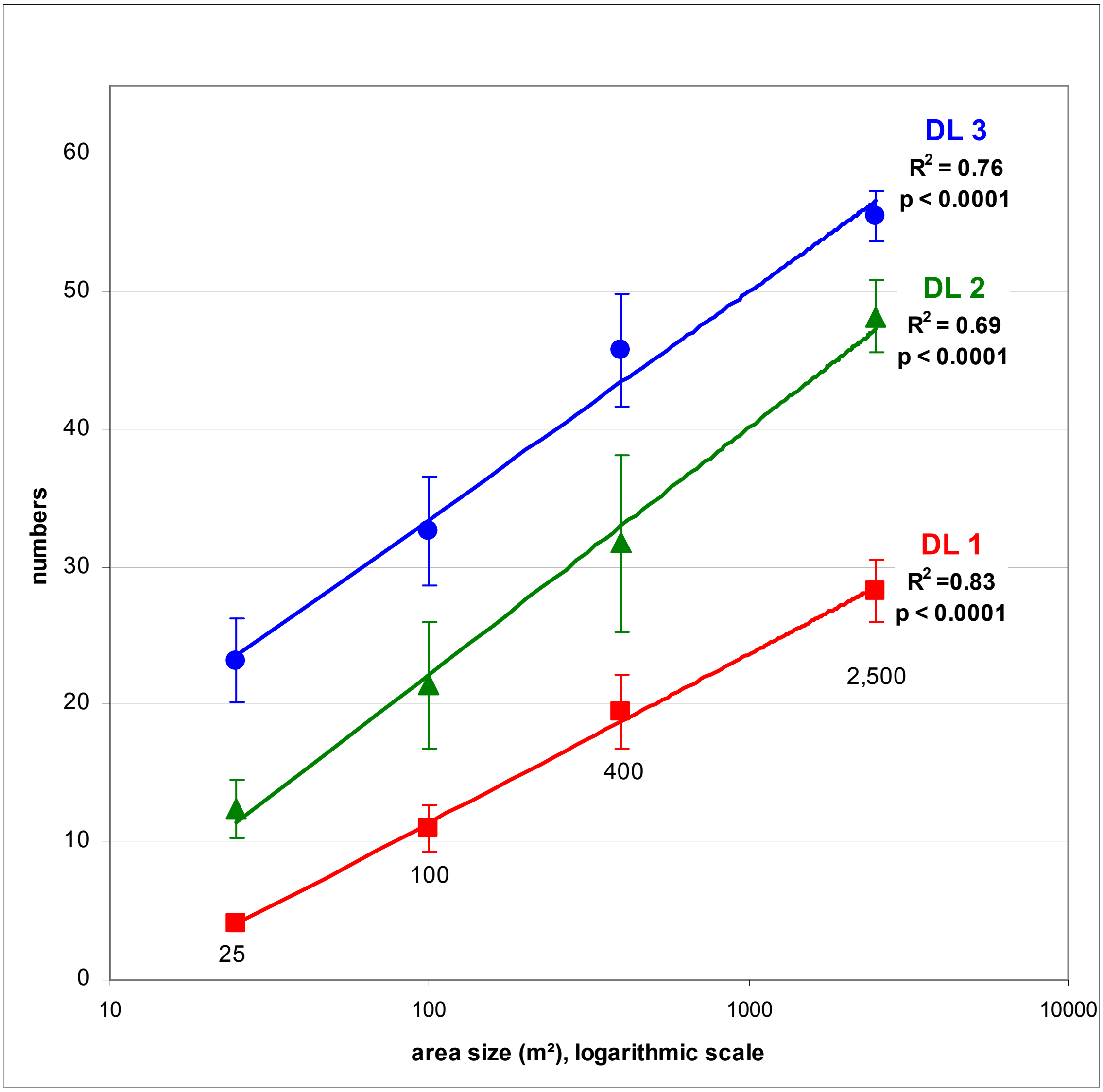

Fig. 5: Mean species number and standard errors (tree regeneration excluded) in the three diversity levels (DL 1, DL 2, DL 3) regarding the area sizes 25 m², N = 3; 100 m², N = 4; 400 m², N = 4 and 2,500 m², N = 4. R²: coefficient of regression.

The greatest portion of the plant species per DL is held by herb-layer species typical of closed forests (group K1.1), and herb-layer species that grow in forests as well as in open vegetation (K2.1), together: DL 1: 71 %, DL 2: 72 %, DL 3: 71 % (Fig. 6). Herbs mainly growing in clearings or at forest edges (K1.2) and herbs growing partly in forests, but mainly in open vegetation (K2.2) occur less frequently, together: DL 1: 3 %, DL 2: 6 %, DL 3: 8 %. Group K2.2 could not be found in stand type DL 1 at all. Shrubs growing partly in forests, but mainly in open vegetation (S2.2) dominate. The proportion of tree-layer species to all species shows a slight decline with increasing diversity level (DL 1: 16 %, DL 2: 13 %, DL 3: 12 %).

In each of the three diversity levels, about 70 % of all vascular plants belong to the phytosociological group 8 'broadleaved woodland and related communities' (Fig. 7; DL 1: 73 %, DL 2: 72 %, DL 3: 70 %). The remainder of sociological groups represent in DL 1 and DL 2 16 %, and in DL 3 20 % of the flora. In DL 3, plants typical of heaths and grasslands created by human or animal activity and plants loosely associated with woodlands reach a higher proportion of the flora (together 12 %) than in DL 1 (together 6 %) and DL 2 (together 7 %). Only one neophyte was found: the Small Yellow Balsam *(Impatiens parviflora)*, native to central Asia, found in site DL 1c. All other vascular plant species encountered are native to central Europe.

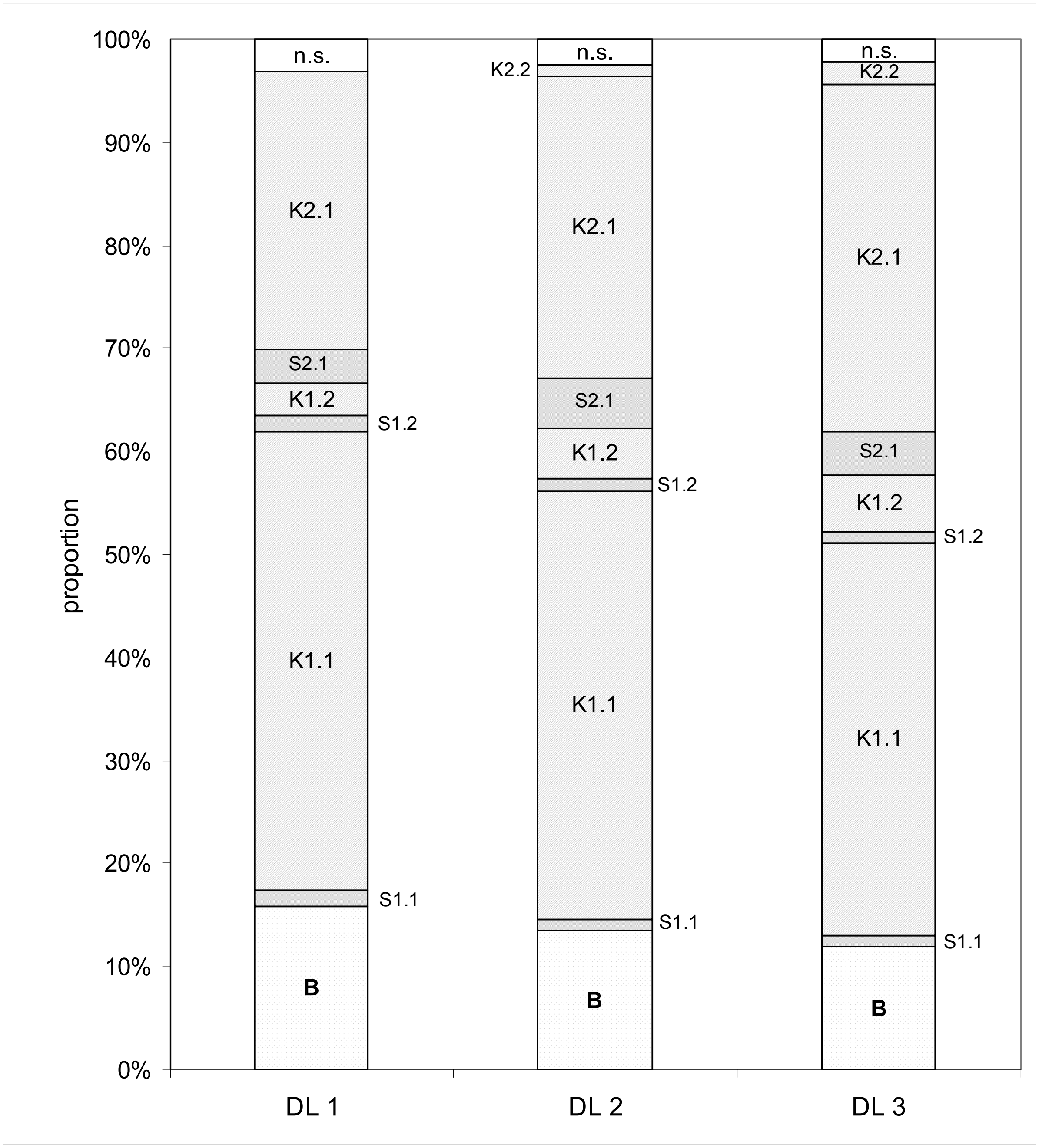

Fig. 6: Proportions (%) of vascular plants characteristic of forests or open landscapes (according to SCHMIDT et al. 2003) in the three diversity levels DL 1, DL 2 and DL 3. The analysis (qualitative evaluation) was done on the basis of the overall species lists compiled for each diversity level (S = shrub layer, K = herb layer. n.s.: not specified, K+S 2.2: partly in forest, mainly in open vegetation, K+S 2.1: in forest as well as open vegetation, K+S 1.2: mainly in forest clearings or in forest fringes, K+S 1.1: mainly in closed forests, B: tree layer).

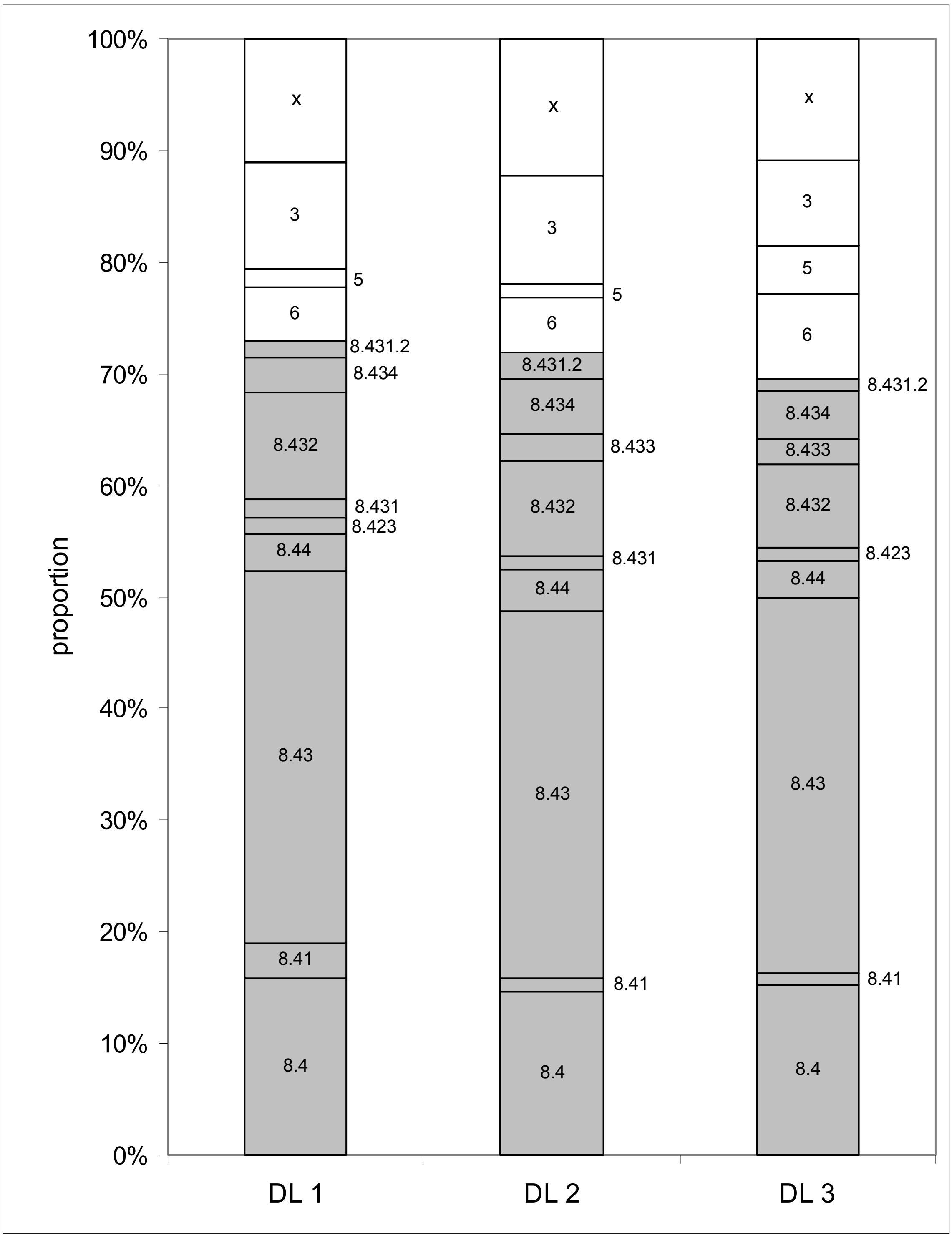

Fig. 7: Proportions (%) of sociological groups (according to ELLENBERG 2001) in the three diversity levels DL 1, DL 2 and DL 3. The analysis (qualitative evaluation) was done on the basis of the overall species lists compiled for each diversity level (x: indifferent plants, 8: broadleaved woodland and related communities, 8.4: Querco–Fagetea, 8.41: Quercetalia robori-petraeae, 8.43: Fagetalia (sylvaticae), 8.44: Prunetalia spinosae, 8.423: Potentillo albae-Quercion petraeae, 8.431: Fagion (sylvaticae), 8.432: Carpinion betuli, 8.433: Alno-Ulmion(minoris), 8.434: Tilio–Acerion pseudoplatani, 8.431.2: Galio odorati–Fagenion, 6: woodland-related herbaceous perennial and shrub communities, 5: heaths and grasslands created by human and animal activity, 3: herbaceous vegetation of frequently disturbed sites).

3.2 Species composition and vegetation units

Forest communities were characterised and classified by 12 vegetation relevées representing typical vegetation conditions of each of the 12 research sites (Tab.1). In the first six relevées (Tab. 1), beech (*Fagus sylvatica*) dominates the tree layer. The other tree species (*Acer pseudoplatanus*, *Acer platanoides*, *Tilia cordata*, *T. platyphyllos*, *Fraxinus excelsior* and *Quercus robur*) are only sporadically interspersed, and do not attain coverage higher than 25 % in the tree layer of the DL 2 research sites. In contrast, in the other six relevées (7-12) beech represents less than 50 % of the tree-layer coverage, in relevée 12 it is lacking totally. All these relevées are clearly richer in canopy species, *Fraxinus excelsior* and *Tilia cordata* occur frequently together with varying proportions of *Tilia platyphyllos, Acer pseudoplatanus*, *Acer platanoides*, *Quercus robur, Carpinus betulus* and *Acer campestre*. Tree-layer data alone can assign the first six relevées to the beech forest alliance (Galio odorati – Fagion), and the second half of the relevées to the oak-hornbeam forest alliance (Carpinion betuli). Shrub-layer vegetation is lacking in the beech forests, while it is slightly better developed in the oak-hornbeam forests (mostly those regenerating *Tilia cordata*).

Regarding the beech forests, relevée 1 (from DL 1a) shows a surprisingly low herb-layer cover (compared to the other relevées) in spring. Even *Anemone nemorosa* – otherwise in beech forests represent with more than 75 % coverage – does not reach 25 % coverage at all. Furthermore, *Hordelymus europaeus* and *Lilium martagon,* two characterising species of the Hordelymo-Fagetum (DIERSCHKE 1989), are absent, while acid-tolerant bryophytes like *Polytrichum formosum* and *Atrichum undulatum* occur frequently. The five other beech forest relevées (2-6) can be divided into two subunits by the presence/absence of *Stellaria holostea, Pulmonaria officinalis, Ranunculus ficaria, Primula elatior, Anemone ranunculoides, Viola reichenbachiana, Lathyrus vernus, Arum maculatum* and *Ranunculus auricomus*. DL 1 and DL 2 research sites are distributed equally in both subunits. In the oak-hornbeam forests, an exact classification by herb and bryophyte layer species is more difficult, since different groups of differential species overlap. Two groups consisting of relevées 7-9 and 10-12 emerge based solely on species numbers. Both subunits contain the species *Polygonatum multiflorum*, *Carpinus betulus*, *Vicia sepium*, *Fragaria vesca*, *Ranunculus lanuginosus*, *Campanula trachelium*, *Stachys sylvatica*, *Galium sylvaticum* and *Arctium nemorosum*, and with noticeable high cover values *Ranunculus ficaria*. Among those species that appear in the present data set to differentiate from beech forests, only two (*Carpinus betulus*, *Galium sylvaticum*) were identified as species characterising the oak-hornbeam alliance by OBERDORFER (1957, 1992) and DIERSCHKE (1986). Other Carpinion-species such as *Stellaria holostea*, *Dactylis polygama*, *Tilia cordata* and *Prunus avium* also occur in the beech forests of the Hainich, but less frequently than in the oak-hornbeam forests. *Sanicula europaea*, *Acer campestre*, *Bromus ramosus*, *Geum urbanum*, *Hieracium murorum*, *Phyteuma spicatum*, *Dryopteris filix-mas* and *Dactylorhiza maculata* frequently grow on decalcified, acidified clay soils with good water supply. These species, in tandem with the soil-dwelling bryophytes *Plagiomnium undulatum*, *Eurhynchium swartzii*, *Brachythecium rutabulum*, *Brachythecium velutinum* and *Fissidens taxifolius* characterise the most species-rich relevées (10-12 from DL 3). Several other species fall between these two groups. *Allium ursinum*, *Dactylis polygama*, *Ulmus glabra* and *Senecio ovatus* connect the species-poor relevée 9 (in DL 2b) to the more species-rich relevées 10-12. The higher cover values of *Alliaria petiolata* in relevée 8 (DL 2d), may indicate both a higher nitrogen supply and a higher degree of disturbance caused by past forest management compared to that in other oak-hornbeam forest research sites.

Tab. 1: Vegetation table of the research sites in Hainich National Park. Relevées 1-3 belong to the Galio odorati–Fagetum (possibly only relevée 1, with placement of relevées 2-3 in the Hordelymo–Fagetum typicum), relevées 4-6 to the Hordelymo–Fagetum lathyretosum, and relevées 7-12 to the Stellario–Carpinetum stachyetosum. Abbreviations for character (C) or differential species (D), follow Dierschke (1986, 1989) (V: alliance, A: association): HF: AC, DA Hordelymo–Fagetum; HFL: DA Hordelymo–Fagetum lathyretosum: HFC: DA Hordelymo–Fagetum circaeetosum; CA: VC Carpinion betuli; SC: DA Stellario–Carpinetum; SCS: DA Stellario–Carpinetum, subassociation group of *Stachys sylvatica*.

Relevé		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Plot no.	DL	**1b**	**1c**	**2c**	**1a**	**2a**	**1d**	**3c**	**2d**	**2b**	**3d**	**3b**	**3a**
Tree layer, cover (%)		94	95	97	96	97	89	96	96	98	97	91	93
Shrub layer, cover (%)		0	1	0	0	0,5	0	0	1	5	3	7	7
Herb layer (spring), cover (%)		24	44	84	86	78	91	76	83	85	83	78	80
Herb layer (summer), cover (%)		25	18	15	29	48	43	35	69	71	63	39	60
Bryophyte layer, cover (%)		0,5	+	0,5	0	+	0,5	r	0	+	0,5	4	8
Tree layer, number of species		2	1	3	2	5	3	5	3	4	7	5	7
Shrub layer, number of species		0	1	0	0	2	0	0	0	3	2	1	3
Herb layer, number of species		21	23	20	23	30	34	39	51	50	62	59	57
ditto, but without tree species		13	19	18	18	25	28	32	44	44	53	50	48
Bryophyte layer, number of species		2	3	2	2	1	2	1	1	1	8	10	9
Total number of species		24	26	22	25	31	36	40	52	51	71	69	66
Tree layer													
Fagus sylvatica		5	5	5	5	5	4	3	3	3	2a	3	.
Fraxinus excelsior		.	.	2a	.	.	.	2a	3	2a	2a	2a	1
Tilia cordata CA		.	.	1	.	+	.	3	2b	3	3	3	3
Acer pseudoplatanus		.	.	.	1	2a	2a	2a	.	2a	1	.	2a
Carpinus betulus CA		.	.	.	.	.	.	2a	.	.	3	2b	3
Acer platanoides		.	.	.	.	2a	2a	.	.	.	2a	.	.
Acer campestre		.	.	.	.	.	.	.	.	.	1	.	2a
Tilia platyphyllos		.	.	.	.	+	.	.	.	.	.	2b	2b
Quercus robur		1	.	.	.	.	.	.	.	.	.	.	2a
Shrub layer													
Tilia cordata CA		.	.	.	.	+	.	.	.	2a	+	2a	2a
Fagus sylvatica		.	1	.	.	+	.	.	.	+	.	.	.
Tilia platyphyllos		.	.	.	.	.	.	.	.	.	1	.	.
Fraxinus excelsior		.	.	.	.	.	.	.	.	+	.	.	1
Acer pseudoplatanus		.	.	.	.	.	.	.	.	.	.	.	+
Herb layer													
Hordelymus europaeus HF		.	r	r	+	+	+	+	1	+	2a	1	1
Deschampsia cespitosa s.str. SC		.	r	+	+	+	+	+	.	+	+	1	2a
Athyrium filix-femina HFC, SC		.	+	r	+	r	+	r	.	r	.	+	r
Lilium martagon		.	r	r	.	r	r	r	+	r	r	r	r
Stellaria holostea CA		.	r	.	r	r	+	2a	3	1	2b	+	2a
Pulmonaria officinalis		.	.	r	.	+	+	+	+	1	r	1	1
Ranunculus ficaria SCS		.	.	.	+	2b	1	2a	3	3	3	2a	2b
Primula elatior		.	.	.	r	+	+	+	+	+	+	+	1
Anemone ranunculoides HF		.	.	.	r	2b	+	1	2a	1	1	1	1
Viola reichenbachiana		.	.	.	r	r	r	r	+	r	+	+	+
Lathyrus vernus HFL		.	.	.	r	r	r	+	+	+	+	+	+
Arum maculatum agg. HF		.	.	.	r	+	r	r	+	r	+	+	+
Ranunculus auricomus agg. HFL		.	.	.	.	r	r	r	+	r	+	+	+
Carpinus betulus CA		r	.	.	.	.	.	r	r	.	+	1	+
Vicia sepium		.	.	.	.	.	.	r	r	r	r	+	+
Fragaria vesca		.	.	.	.	.	.	.	r	r	+	+	+
Ranunculus lanuginosus		.	.	.	.	.	.	.	+	+	+	+	+
Campanula trachelium		.	.	.	.	.	.	.	2a	r	+	+	+
Stachys sylvatica HFC, SCS		.	.	.	.	.	.	.	r	r	r	r	.
Galium sylvaticum s.str. CA		.	.	.	.	.	.	.	r	r	.	+	+
Arctium nemorosum		.	.	.	.	.	.	.	r	+	r	r	r
Listera ovata		.	.	.	.	.	.	.	r	.	r	r	r
Allium ursinum		.	.	.	+	.	.	.	.	2a	2a	1	2a
Dactylis polygama CA		.	.	.	.	.	r	.	.	r	1	1	1
Ulmus glabra		.	.	.	.	.	.	.	.	+	+	r	+
Senecio ovatus		+	.	.	.	.	r	.	.	+	r	r	+
Sanicula europaea		.	.	.	.	.	.	.	.	.	+	1	1
Acer campestre		r	.	.	.	.	.	.	.	.	+	+	+
Bromus ramosus s.str.		r	.	.	.	.	.	.	.	.	+	r	1
Geum urbanum		.	.	.	.	.	.	.	r	.	+	+	+

Tab. 1: Continued.

Relevé		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Plot no.	DL	**1b**	**1c**	**2c**	**1a**	**2a**	**1d**	**3c**	**2d**	**2b**	**3d**	**3b**	**3a**
Herb layer (continuation)													
Hieracium murorum		.	.	.	.	.	.	.	.	.	+	+	+
Phyteuma spicatum HFL		.	.	.	.	.	.	.	.	.	r	r	+
Dryopteris filix-mas		.	r	.	.	.	+	.	.	.	+	r	r
Dactylorhiza maculata subsp. maculata		.	.	.	.	.	.	.	.	.	r	r	r
Asarum europaeum HFL		.	.	.	.	.	1	+	1	1	1	.	.
Mercurialis perennis HF		.	.	.	.	.	r	+	2a	r	+	.	.
Aegopodium podagraria		.	.	.	.	.	.	r	2a	3	2a	.	.
Geranium robertianum s.str.		.	.	.	.	.	.	.	r	r	r	.	.
Sambucus nigra		.	.	.	.	.	.	.	r	+	.	.	.
Galium aparine		.	.	.	.	.	.	.	r	r	.	.	.
Urtica dioica HFC, SCS		.	.	.	r	.	.	.	r	r	.	.	.
Others													
Anemone nemorosa		2b	3	5	5	3	5	4	2b	3	3	4	3
Fraxinus excelsior		1	+	2a	2a	2b	1	2a	2a	2a	1	1	2a
Acer pseudoplatanus		1	+	+	1	+	3	2a	1	2a	1	1	1
Acer platanoides		+	.	1	1	3	1	1	1	2a	1	1	1
Fagus sylvatica		2a	2a	2a	1	+	1	1	1	2a	1	2a	+
Lamium galeobdolon s.str.		.	r	+	2a	1	.	1	2a	1	1	1	1
Convallaria majalis		2a	r	r	.	.	r	r	+	+	1	+	1
Carex sylvatica SCS		r	r	+	.	r	+	r	r	+	+	1	1
Milium effusum		r	r	.	+	+	+	+	r	+	1	r	+
Tilia spec. CA		r	.	r	r	r	r	+	r	+	+	+	+
Crataegus laevigata HFL		r	r	r	r	r	r	r	+	r	+	r	r
Dryopteris dilatata		.	.	+	.	r	r	r	.	r	r	+	r
Oxalis acetosella SC		.	+	.	.	+	.	.	.	.	.	.	.
Hedera helix		.	r	.	.	r	.	+	.	r	r	+	+
Circaea lutetiana HFC, SC		.	.	.	+	.	.	.	.	+	.	r	.
Prunus avium CA		+	r	.	.	.	r	r	r	.	r	+	.
Alliaria petiolata		r	r	.	.	.	+	.	2a	.	r	r	.
Poa nemoralis		r	.	.	.	.	r	.	.	.	+	+	r
Lonicera periclymenum		.	.	r	r	.	.	r	r	+	.	r	.
Chaerophyllum temulum		.	.	.	.	.	.	.	+	.	.	.	r
Euonymus europaea		.	.	r	.	r	.	r	.	r	r	.	.
Scrophularia nodosa		.	.	.	.	r	.	r	.	.	r	r	r
Brachypodium sylvaticum		r	.	.	.	.	+	.	.	.	.	.	r
Maianthemum bifolium		r	r	.	.	.	.	.	r	.	r	.	.
Cardamine pratensis s.l. SCS		.	.	.	.	.	.	r	r	.	r	.	r
Lathraea squamaria		.	.	.	.	r	.	.	r	.	r	.	.
Quercus robur		.	.	r	.	.	.	.	.	.	r	.	r
Melica uniflora		.	.	.	.	.	.	r	.	.	.	r	.
Daphne mezereum		.	.	.	.	r	.	r	.	.	.	.	.
Epipactis helleborine		.	.	r	.	.	.	.	.	.	.	.	r
Bryophyte layer													
Polytrichum formosum		+	r	r	r	.	.	.	.	.	.	.	.
Atrichum undulatum		+	r	+	r	+	+	r	.	.	+	1	+
Eurhynchium striatum		.	.	.	.	.	r	.	r	+	+	1	2a
Plagiomnium undulatum		.	.	.	.	.	.	.	.	.	r	+	1
Eurhynchium swartzii		.	.	.	.	.	.	.	.	.	+	+	r
Brachythecium rutabulum		.	.	.	.	.	.	.	.	.	+	r	r
Fissidens taxifolius		.	.	.	.	.	.	.	.	.	+	r	r
Brachythecium velutinum var. velutinum		.	.	.	.	.	.	.	.	.	r	r	r
Eurhynchium praelongum		.	.	.	.	.	.	.	.	.	.	r	r
Thuidium tamariscinum		.	.	.	.	.	.	.	.	.	.	r	r

Only in relevé No. 1: *Calamagrostis arundinacea* r, *Carex muricata agg.* R; No. 2: *Impatiens parviflora* +, *Gymnocarpium dryopteris* +, *Dicranella heteromalla* M r; No. 8: *Geranium dissectum* r, *Moehringia trinervia* r, *Galium odoratum* r, *Orchis mascula* r; No. 9: *Actaea spicata* r, *Rubus idaeus* r; No. 10: *Festuca heterophylla* r, *Taraxacum sect. Ruderalia* r, *Lapsana communis* r; No. 11: *Hypericum perforatum* r, *Rubus fruticosus agg.* r, *Carex muricata agg.* r, *Ajuga reptans* r, *Mnium hornum* M r; No. 12: *Paris quadrifolia* +, *Corydalis cava* r, *Gagea lutea* r.

4. Discussion

4.1 Flora and floristic diversity

The forest-plant classification of SCHMIDT et al. (2003) as well as the sociological-group classification of ELLENBERG (2001) clearly show that the research sites in the Hainich area are characterised by a typical forest flora, with only a few species associated with open landscapes. In comparable unmanaged deciduous forest stands (forest nature reserves) with high base-saturation (limestone or basalt as bedrock), the amount of herb-layer species characteristic of closed forests varies between 50 % and 70 % of the overall flora (MÖLDER 2005, SCHMIDT 2005). Particularly in deciduous forests, this proportion increases with the amount of time since conversion from managed to unmanaged status, and decreases under conditions of intensive management (BRUNET et al. 1996, 1997; WULF 1997; LAWESSON et al.; 1998; GRAAE & SUNDE 2000; SCHMIDT M. et al. 2003b; WULF 2003; EBRECHT 2005; SCHMIDT 2005; SEBASTIÀ et al. 2005). Additionally, the high proportion of typical forest species indicates considerable habitat continuity in the research area (SCHMIDT M. et al. 2003b). However, the degree of continuity of forest cover is much more important than the forest management status (GRAAE & SUNDE 2000). Populations of forest-dependent herbs may be as old as mature trees in the forest (TAMM 1972, INGHE & TAMM 1985, POLLMANN 2000, NICOLË et al. 2005). Survival of the most forest-dependent species is possible only in ancient forests without strong human impact (ZACHARIAS 1993, WULF 1997, LAWESSON et al. 1998, HERMY et al. 1999, HONNAY et al. 1999, WULF 2003). The poor ability of these old-growth forest species to colonise new forest sites may be attributed to a complex of interacting variables: limited dispersal abilities (many have a short-distance dispersal strategy), low diaspore production and recruitment problems (e.g. low competitive ability, HERMY et al. 1999, VERHEYEN et al. 2003, VERHEYEN & HERMY 2004). Species with heavy seeds, transient seedbanks, ant-dispersed seeds, early and short flowering time, low stature, and high extent of vegetative reproduction are more common in older forests (GRAAE & SUNDE 2000). Therefore, forest continuity should be a primary focus of nature conservation, spatial planning and forest management.

No differences in species affiliations to forest sites or forest communities were determined among the three diversity levels. However, plants of the forest species group 2.2 (growing partly in forests, but mainly in open vegetation) were exclusively found in the diversity levels (DL) 2 and 3. Additionally, the DL 3 research sites showed higher portions of ELLENBERG's group 5 “heaths and grasslands determined by human and animal activity” and 6 “woodland-related herbaceous perennial and shrub communities”. The occurrence of these groups may be an indication of a history of disturbance events (ELLENBERG 1996, SCHMIDT 2005), probably by a more distinctive ancient coppice with standards system in these stands. This system, which creates canopy gaps at frequent intervals (associated in part with grazing), promotes the occurrence of species characteristic of open landscapes (GEB et al. 2004, STEGMANN & SCHMIDT 2005). However, some forest-dependent species can benefit from coppicing: WULF (1997) presents results from northeastern Germany that verify the clear association of some geophytes, e.g. *Anemone ranunculoides*, *Circaea lutetiana* and *Paris quadrifolia* (which all occur in all diversity levels) with ancient woodlands with a history of coppicing.

The slope of the species-area relationship found in the present study is consistent with the descriptions of DIERSCHKE (1994) and ROSENZWEIG (2000). Both abiotic factors and niche diversification play a role in mediating species diversity (SCHMIDT 2005). Relevées from various parts of Central Europe reveal that species richness in beech forests is positively correlated with base-saturation (MAYER 1974, BRUNET et al. 1996, ELLENBERG 1996, LEUSCHNER 1999, SCHMIDT submitted). As predicted by the species-pool hypothesis (ZOBEL 1997), this relationship also arises in floristic inventory of larger sample plots.

A comparison of floristic data calculated for the Hainich research sites with data from unmanaged forest nature reserves in beech forests and oak-hornbeam forests on basic and nutrient-rich soils showed a broad range of species richness levels (Tab. 2). The lowest values (40-50 species/ha) are mainly found in Milio-Fagetum or Galio-Fagetum sites or on homogeneous sites within the Hordelymo-Fagetum (Hohestein). Following the environmental heterogeneity hypothesis (HUSTON 1994), species diversity should increase with local heterogeneity in topography, soil-nutrient status, and water availability. This is true e. g. for forest nature reserves like Hasbruch, Mittlere Ith and Hünstollen, where mean species richness of 60-70 species/ha can be found. Finally, higher species diversity can be expected in ecosystems with intermediate disturbance than in undisturbed forests (CONNELL 1978, DECOCQ et al. 2004). The interplay of environmental heterogeneity and disturbance (GRACE 1999) could explain the highest species richness in the Hainholz forest nature reserve (92 species/ha) out of all forest nature reserves so far studied in Germany (SCHMIDT 2003, 2005). In the Hainich area, we calculated mean species numbers between 64 and 75 species/ha in

DL 2 and DL 3, perhaps indicating environmental heterogeneity or disturbance effects, this despite the careful selection of homogeneous and undisturbed research sites. Future research within the project should clarify whether site conditions, forest history or other mechanisms (e.g. biotic interactions) are responsible for this species richness.

Tab. 2: Floristic diversity of vascular plants in unmanaged forest nature reserves compared to the research sites in Hainich National Park. N: Number of analysed subplots (per ha). R: mean Ellenberg reaction value of the reserves' flora. Data from SCHMIDT (1999, 2003, 2005) and MÖLDER & SCHMIDT (2006). *data are extrapolated, hence no means are available.

	N	Species richness (±SE)	R	Forest communities
Landwehr	13	46.2 ±3.4	5.2	*Milio-Fagetum,* *Stellario-Carpinetum*
Hasbruch	31	75.9 ±3.3	5.5	*Stellario-Carpinetum*
Großer Freeden	22	41.5 ±1.3	5.5	*Hordelymo-Fagetum,* *Galio-Fagetum*
Wattenberg/Hundsberg	23	42.5 ±2.4	5.9	*Hordelymo-Fagetum,* *Galio-Fagetum*
Hohestein	13	38.4 ±2.1	6.3	*Hordelymo-Fagetum*
Mittlere Ith	6	62.2 ±2.7	6.4	*Hordelymo-Fagetum*
Hainholz	26	92.0 ±3.7	6.5	*Hordelymo-Fagetum,* *Carici-Fagetum*
Hünstollen	29	58.9 ±2.7	6.6	*Hordelymo-Fagetum*
Hainich, DL 1	4	42.7*	6.3	*Galio-Fagetum,* *Hordelymo-Fagetum*
Hainich, DL 2	4	64.4*	6.6	*Hordelymo-Fagetum,* *Stellario-Carpinetum*
Hainich, DL 3	4	74.5*	6.5	*Stellario-Carpinetum*

Aside from these potential causes of higher diversity, the present results seem to be consistent with hypotheses of positively correlated tree-layer and herb-layer species richness. However, MCCUNE & ANTOS (1981) as well as BRADFIELD & SCAGEL (1984) found low correlations between vegetation layers in coniferous forests in Montana and British Columbia. In Central Europe, HERMY (1988) detected a high correlation between vegetation strata in deciduous woodlands in Belgium, and LEUSCHNER (1999) found a positive relationship between tree-layer and herb-layer diversity in southern German forest communities on the basis of vegetation relevées arranged by OBERDORFER (1992). In deciduous Estonian forests INGERPUU et al. (2003) found that the species richness of both bryophyte and herb layers were significantly positively correlated with the tree species pool. FERRETTI et al. (2006) point out that stand variables (particularly the number of tree species in the dominant storey) were significant predictors of the mean number of vascular plant species in their plots located throughout Italy. In contrast to the above-mentioned authors and the results presented in this study, non-correlation or weak correlations were found between tree-layer and herb-layer diversity by EWALD (1997, 2000, 2002) in mountain forests of the Bavarian Alps, NEUMANN & STARLINGER (2001) on plots all over Austria and AUBERT et al. (2004) in the Normandy (France).

4.2. Syntaxonomical classification and species richness of the forest communities

The map of potential natural vegetation in Germany and Europe (BfN 2000, BOHN et al. 2003), shows the Hainich to be covered by species-rich beech forests (alliance Galio odorati-Fagion), but connected to the Carpinion betuli of the Thuringian basin, a dry and warm area where beech is absent or rare. The transient situation between subatlantic beech and subcontinental oak-hornbeam forests might partly explain the coexistence of forest communities rich in tree species in our research area (FRECH 2006).

Both herb and bryophyte composition of the Hainich research sites allow a first rough classification of the forest communities. This classification would surely be better documented with more relevées from all over the Hainich area, especially to identify small-scale gradients of varying loess cover with different water and nutrient supply as well as to clarify the impact of past forest management. Concordant with results from DIERSCHKE (1989), all beech-rich research sites in the present study (relevées 1-6) can be assigned to the suballiance Galio odorati-Fagenion (Woodruff beach forests). The moisture indicators *Lamium galeobdolon*, *Carex sylvatica*, *Milium effusum* and *Oxalis acetosella* clearly distinguish the Galio odorati–Fagenion and beech forests on warm and dry limestone slopes (suballiance Cephalanthero-Fagenion). With the exception of *Hordelymus europaeus* and *Lilium martagon*, all differential species of the Hordelymo-Fagetum (*Arum maculatum*, *Anemone ranunculoides*, *Mercurialis perennis*) are absent from relevées 1-3, thus a classification as Galio odorati-Fagetum is also possible. The gradual transition between the Galio odorati–Fagetum and the Hordelymo-Fagetum with varying rates of differential species also allows a classification of relevée 1 to the Galio odorati-Fagetum and relevées 2 and 3 as Hordelymo-Fagetum typicum. Considerably clearer is the assignment of relevées 4-6 to the Hordelymo-Fagetum lathyretosum by the presence of the character species of the association *Hordelymus europaeus*, *Arum maculatum*, *Anemone ranunculoides* and *Mercurialis perennis* (only relevée 6) as well as the differential species of the subassociation like *Lathyrus vernus*, *Ranunculus auricomus*, *Lilium martagon*, *Crataegus laevigata*, *Daphne mezereum* and *Asarum europaeum* (DIERSCHKE 1985, 1989). According to HOFMANN (1965) and AHRNS & HOFMANN (1998) the spring vetch beech forest (Lathyro-Fagetum) is the most common forest community of the Hainich area and typifies at a broad scale the potential natural vegetation (pnv) as well as the potential site-adapted vegetation (psv) sensu LEUSCHNER (1997).The difficulty in obtaining an unambiguous classification for species-rich beech forests and oak-hornbeam forests in Hainich National Park was also reported by DIERSCHKE (1985, 1986) for southern Lower Saxony. On waterlogged soils as well as on shallow, dry soils the portion of beech is lower and other species like *Carpinus betulus*, *Tilia cordata*, *T. platyphyllos*, *Acer campestre, Sorbus torminalis,* and *Quercus robur* are more dominant (ELLENBERG 1996, LEUSCHNER 1998, SCHMIDT 2000). In addition to water availability, the frequency and dominance of *Fagus sylvatica* is strongly affected by forest management status: under a coppice with standard system or (pure) coppicing, beech decreases rapidly. This decline - particularly in consequence of low sprouting ability of beech - is more pronounced in subatlantic than in subcontinental areas (ELLENBERG 1996). The continuous regeneration of *Fagus sylvatica* in the oak-hornbeam forests of the Hainich underlines the assumption that beech will increase if forest management ceases. Increasing portion of beech occurs in many high forest stands formerly used as coppices with standards or during succession in unmanaged forest nature reserves (BLOSAT & SCHMIDT 1975, DIERSCHKE 1985, 1986, OBERDORFER 1992, ELLENBERG 1996, LEUSCHNER 1997, GEB et al. 2004, SCHMIDT 2000, 2005, STEGMANN & SCHMIDT 2005).

In the Hainich area, species richness within the Stellario-Carpinetum is greater than that in the Hordelymo-Fagetum. This pattern was also found in other regions, where Hordelymo-Fagetum stands are always poorer in species than Stellario-Carpinetum stands (Tab. 3). In the relatively oceanic Westphalia region, species numbers of the Stellario-Carpinetum are about 60 % higher than species numbers of the Hordelymo-Fagetum. By contrast, in Lower Saxony (including the Harz Mountains) the species numbers of the Stellario-Carpinetum are merely 7-36 % higher. Vegetation relevées made by OBERDORFER (1992) and re-analysed by LEUSCHNER (1999) showed no differences in herb-layer diversity among the constant species, while differences were revealed between the tree layers of the Hordelymo-Fagetum and the Stellario–CarpInetum. The attempt to explain this regional trend by the geographical centre of these forest communities (Hordelymo-Fagetum: Central European, Stellario-Carpinetum: subatlantic) is contradictory to the results from the Hainich area. Hence, the differences in species richness between the Stellario-Carpinetum and the Hordelymo-Fagetum may have non-biogeographical causes.

Tab. 3: Comparison of species numbers of species-rich beech forests (Hordelymo-Fagetum) and oak-hornbeam forests (Stellario-Carpinetum). n: Number of relevées.

Research area	Richness, beech forest	N	Richness, oak-hornbeam forest	N	Source
Western Westphalia (Münsterland)	22 (100 %)	16	35 (159 %)	55	LOHMEYER 1967
Eastern Westphalia (Lippe)	25 (100 %)	72	40 (160 %)	4	GOLISCH 1996
Eastern Lower Saxony	19 (100 %)	43	21 (111 %)	100	SOMMER 1971
Southern Lower Saxony	29 (100 %)	305	39 (134 %)	355	DIERSCHKE 1985
Harz Mountains, foothills	22 (100 %)	81	30 (136 %)	35	ZACHARIAS 1996
Harz Mountains	27 (100 %)	47	29 (107 %)	48	PFLUME 1999
Hainich	27 (100 %)	6	58 (215 %)	6	this study (Tab. 1)

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