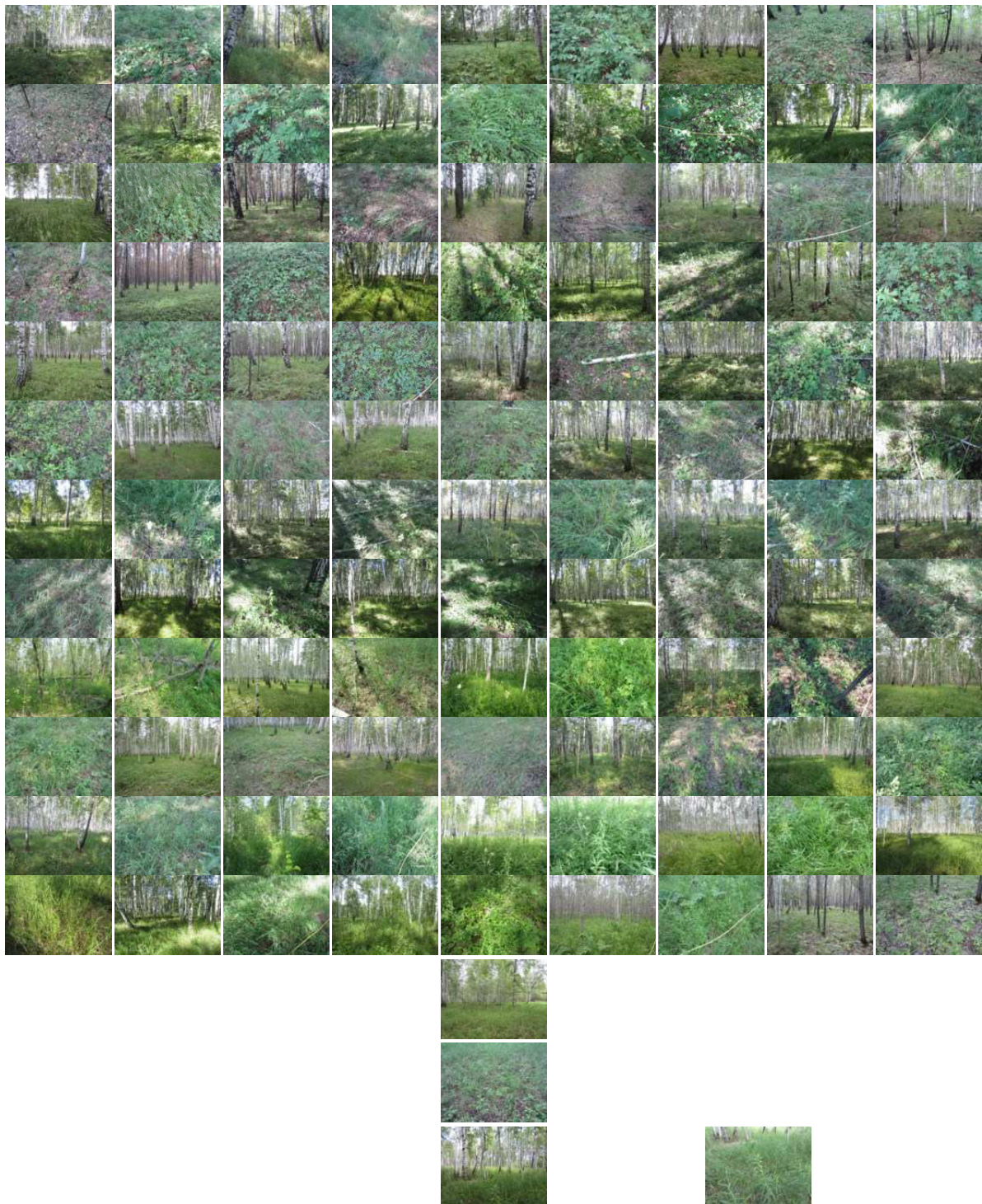


Birch forests in Western Siberia – a modern analogue to Pre-Boreal European forests

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Masterarbeit

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Birch forests in Western Siberia – a modern analogue to Pre-Boreal European forests

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Abstract

Historically, the Central European landscape was characterised by vast forests – open ecosystems were scarce, however. During the early Holocene massive changes in the landscape structure resulted in the emerging of a variety of open ecosystems. A practical method to better understand the development of these processes is to study modern analogues, which can be found in the ecosystems of West Siberian forests. The aim of this work is to study habitat-level floristic diversity and its environmental correlates in the birch forests of the hemiboreal zone and thus them as modern analogues.

Therefore, we studied open birch forest and grassland vegetation in the east of the Ural in the southern part of the Oblast Tyumen. By analyzing the species data using cluster analyses we identified four forest types with varying structural characteristics, revealing that the principal gradients were humidity and the grade of canopy cover. The species richness was also most affected by the canopy-transmitted light and furthermore by humidity. Besides typical forest species, comparing the samples with Central European classification, our species inventory showed a fairly high amount of open landscape species, especially of wet grassland. The nearby grassland vegetation on the other hand harvested a species range which is known in Central Europe from open landscapes, especially from dry grassland.

We explain this shift of open landscape species into the forest by the theory of relative site constancy of plants. The ecological demands of wet grassland species are met by West Siberian birch forests because they provide an open structure and a moist and temperate-controlled microclimate in the otherwise hot and dry continental summer climate.

According to these results it is easy to imagine that analogue to the modern forests of today's Siberia, early Holocene open-canopy forests of Central Europe had a similar structure and therefore provided appropriate growing conditions for a species rich flora of light-demanding species. Thus, our results give further evidence that the flora of today's open ecosystems have their origin in open forests.

Keywords: Modern Analogues • Forest Steppe • West Siberian Plain • Tyumen • Open Canopy •
Habitat shift

Introduction

Historically, the Central European landscape was characterized by vast forests (Ellenberg & Leuschner 2010). Several studies also consider that some parts of the vegetation were opened up by browsing, grazing, and trampling of large herbivores (e.g. Beutler 1996, Vera 2000) resulting in a forest-steppe with open woodlands of coniferous (*Larix decidua*, *Pinus sylvestris*) and small-leaved deciduous trees (*Betula pendula*, *Populus tremula*) (Svenning 2002, Svenning et al. 2008). During the early Holocene massive environmental changes in the landscape structure resulted in the emergence of mixed oak forests with the new expanding broad-leaved deciduous trees of the genus *Quercus*, *Ulmus*, *Tilia*, *Acer*, and *Fraxinus* (Ellenberg & Leuschner 2010). Additionally, the increasing human impact resulted in massive changes. A momentous transition took place in the early Holocene when many human cultures changed from a lifestyle of hunting and gathering to one of agriculture and settlement: the Neolithic Revolution. People also started to practice the slash-and-burn method for urbanization (Bar-Yosef 2008). This favoured the emergence of a variety of open ecosystems (Ellenberg & Leuschner 2010). These transitions must have had a considerable effect on the biodiversity of flora and fauna. Some species disappeared; some other survived as relicts at certain regions (e.g. *Kadenia dubia*, *Filipendula vulgaris*) and some could recover their past extend as for example *Sanguisorba officinalis* (Burkart 2001, Ellenberg & Leuschner 2010, Köhl & Gobet 2010). Nowadays, open landscape biotopes are disproportionately richer in species than forest habitats (Ellenberg & Leuschner 2010). As interesting as these developments are, it is very difficult to trace them accurately. The main instrument for reconstructing vegetation is to study and identify pollen. However due to strong difficulties to determine vegetation up to species level in some genera and families, data for this period are scarce (Beug 2004). This is especially the case for herbaceous plants which constituted the biggest part of the vascular plant diversity in Central European forests (Ellenberg & Leuschner 2010). Another way to study the history of the development of the flora is to study modern analogues (Furyaev et al. 2001, Chytrý 2010). The tree species composition of West Siberian forests seems to be very similar to the pre-boreal open-canopy forests of Central Europe: open forests of small-leaved deciduous trees, dominated by *Betula pendula*. By analyzing fossil pollen Kuneš et al. (2008) were able to show that the vegetation of the Western Sayan Mountains in southern Siberia constitutes a modern analogue to Pleistocene European forests. High similarities in tree species composition and structure of present West-Siberian forest and Early-Holocene European forest enable us to assume an analogue for our study area too. Furthermore, the modern continental climate of southern West Siberia shows very similar characteristics like the Central European predominating climate during late Pleistocene and early Holocene (Frenzel et al. 1992).

The hemiboreal forest is the intermediate zonal type between the true boreal forest (taiga) in the north and the steppe zone in the south, establishing a relatively narrow geographical subzone between latitudes 52° and 58° N (Ermakov et al. 2000). The flora consists of about 400 species of vascular plants (Ilyina et al. 1985). This high number is owed to the intermediate position of the zone: it shows some similarities to boreal flora, with many taiga species near their southern distributional limits, and to some steppe species at their northern limits (Nimis et al. 1994). While in boreal forests moisture demanding dark-coniferous trees such as *Abies sibirica*, *Picea obovata*, and *Pinus sibirica* occur, light coniferous and small-leaved trees as *Pinus sylvestris*, *Betula pendula*, and *Populus tremula* dominate the warmer and drier hemiboreal forest (Chytrý 2008). Beside tree species

composition also the herbaceous layer shows significant differences. Hemiboreal forests have a well-developed herb layer which is rich in species of temperate distribution, but poor in boreal species. This is attributable to a high fertility of the soils and good light penetration due to poor closure of the canopy (Ermakov et al. 2002). Forests of the taiga do not promote such a favourable environment for the herbaceous layer and are generally poorer in species (Chytrý 2008).

In relation to the size of this zone it is rather poorly studied. Information about patterns of floristic differentiation, species richness and vegetation–environment relationships at finer scales are scarce. A large-scale study of Ermakov et al. (2000) is an exception which provides a detailed picture of floristic diversity for the entire southern Siberian hemiboreal forest zone. Furthermore, some research was carried out in adjacent regions – on the western and eastern foothills of the Southern Ural Mountains as well as in the southern Urals (Chytrý 2008 & 2010).

The aim of this work is to study habitat-level floristic diversity and its environmental correlates in the birch forests of the hemiboreal zone and thus them as modern analogues.

Our research questions are the following:

- i) How is the herb vegetation of West Siberian birch forests characterised concerning its site requirements and species composition?
- ii) To which extend does the ecological site requirements of identical species in Central Europe and in Western Siberia differ?
- iii) Does the modern analogue give further evidence that Pre-Boreal open-canopy forests in Central Europe were rich in light-demanding species and thus were the origin of the flora of our later open ecosystems?

Study area

This study was conducted in southwestern Siberia (Russia), east of the Ural in the southern part of the Oblast Tyumen (Fig. 1). Geographically the area belongs to the West Siberian Lowland. Therefore, the topography shows a flat surface (Koronovsky 2002). The igneous bedrock consists of Palaeozoic rocks, which are overlain by Mesozoic and Cenozoic sedimentary deposits. These Quaternary deposits range from 200 to 250 m thickness covering the West Siberian Plain (Volko & Oliunin 1993). The region is characterised by a continental climate with a mean temperature of -17.05 °C in January to a mean temperature of +18.07 °C in July, giving an annual mean temperature of -1.02 °C. Annual precipitation lies around 500 mm, which supports a forest-steppe landscape consisting of a mosaic of agriculture, meadows and hemiboreal forests (WMO n.d.). Focus in this study is the forest – commonly open birch forest (*Betula pendula*) (Nimis et al. 1994), rich in structure due to high fire frequency and a low intensity of forestry use. *Populus tremula* may accompany birch in forest communities, especially on rich, wet soil it can be abundant, but it rarely becomes dominant (Ilyina et al. 1985).

Along a south-north transect, three test areas were randomly chosen – area one (TA1) in the north of Tyumen city around the village Kaskara on 68 m a.s.l. (average altitude of the plots), area two (TA2) close to Omotinskiy, 137 m a.s.l. and area three (TA3) close to Ishim, also 137 m a.s.l. The three areas were chosen considering different climatic, eco-zonal and agricultural attributes for giving a representative example of this west Siberian area (Fig. 1).

Test area one is located in the pre-taiga zone of deciduous forests with prevailing grey forest soils and degraded Chernozems but also wet organic soils under agricultural use. The region represents the northern limit of profitable agriculture; insofar it does not offer favourable conditions for agricultural use. This is the reason why soils with favourable growing conditions are in agricultural use and forest sites are restricted to less potentially productive soils. They can be found mainly in the transition zone between degraded Chernozems and poor Regosols on sandy alluvial soils of the river Tura and on Gley and peat soils in the north of the test area. The **second test area** is located in the northern part of the forest-steppe zone with prevailing highly fertile Chernozems. This area provides the best soil qualities for arable land use within the region and shows also a highly developed and profitable agriculture. Due to high abundance of productive growing sites, overall agrarian structure is not everywhere intensive and forest can also be found on Chernozems, however mainly on gleyficated Chernozems. Together with open vegetation types they build wide meadow-forest mosaics. The **third test area** represents the southern part of the forest steppe with also favourable conditions for agriculture. Again forests are suppressed to agricultural unfavourable sites, partly on Gley soils. The forests were the most humid and the richest in structure of the three test areas.



Fig. 1: Location of the three test areas. Zones from Schultz (2000).

Methods

Field work

In the end of July and during August 2012 we sampled in the three test areas birch forests at 61 sites and grassland at 66 sites, using 10×10 m plots. We placed them in homogeneous vegetation, avoiding disturbed or ecotonal places. At each plot, we recorded all vascular plants (taxonomy and nomenclature according to Cherepanov 1995) and estimated their percentage cover. In the forest, we also estimated the percentage cover of each structural layer, divided into tree layer one and two (tree1 & tree2), shrub and herb layer and cover of coarse woody debris (CWD). Due to the absence of bryophytes and lichens in most of the plots, they were not considered in this study. At all plots, we harvested the aboveground biomass of the field layer as mixed samples of five randomly chosen 0.1 m^2 squares on the plot. After collecting, samples were air-dried and weighed. Moreover we recorded following structural and environmental variables: altitude and position was documented by the GPS-receiver Garmin etrex vista HCx, moreover we measured in situ soil pH (using purified water as measuring solution) and electrical conductivity with a mobile measure instrument (HANNA instruments Combo pH & EC). With an electronical altimeter for recording the height of trees, we sampled the average height of each layer by taking 10 samples. Using a Pürckhauer (geological drill) we determined the soil type of each plot.

Data analyses

For a first overview of the vegetation data forest species were classified using the “Classification of Continental Hemiboreal Forests of Northern Asia” (Ermakov et al. 2000).

To define different forest types of the vegetation data set, a numerical classification, using Sørensen-Index as similarity measure and Farthest Neighbour as cluster algorithm was conducted. Prior to all analyses, all species abundances were square-root transformed and species with frequencies lower than five percent were excluded. The classification analyses divided the plots into five groups. Group one and two were merged due to the lack of ecological delimitation. The final classification was post processed by hand. In order to detect structural or environmental differences between the forest types, they were tested for significant differences by One Way Analysis of Variance (ANOVA), in case of normal distribution (Shapiro-Wilk Test of Normality, $P > 0.05$), in case of non-normality ($P \leq 0.05$) by Kruskal-Wallis Test. If significant differences appeared ($P \leq 0.05$), parametric Posthoc-Tukey Tests (Hothorn et al. 2008) for normal distribution and single Kruskal-Wallis Tests for non-normal distribution were appended. For each sample, the mean Ellenberg’s indicator value for humidity, light and nutrient adaption was calculated and also tested for differences in means (Ellenberg et al. 2001). For the detection of significant indicator species for each forest type and for each type of vegetation, the Indicator Species Analysis was performed (Dufrêne & Legendre 1997), which takes account of relative frequencies and abundances of each species in each type. An Indicator value (IV) is assigned to each species, showing its affinity to a certain type ranging between 0 (low affinity) and 100 (high affinity). The sufficient gradient length (total inertia 2.832) allowed a Detrended Correspondence Analysis (DCA) as a method of indirect gradient analysis (Leyer & Wesche 2007). To find out which environmental variables possessed the highest explanatory power for species richness in the forest, a Linear Model (LM) was carried out. Several environmental parameters (predictor variables) were included to the full model (Tab. 1) – non-

significant predictors were excluded from the final model by stepwise backward-selection ($P > 0.05$). The classification into forest and grassland species follows European literature (Oberdorfer 2000). Sociological units were grouped to “forest” – Querco-Fagetea, Alnetea glutinosae, Vaccinio-Piceetea; “near forest” – Trifolio-Geranieta sanguine, Epilobietea; “wet grassland” – Molinietalia caeruleae; “dry grassland” – Sedo-Scleranthetea, Festuco-Brometea, Arrhenatheretalia and “ruderal” – Agropyretea, Chenopodietea, Plantaginetea, Artemisietea. Species which did not occur in Europe were not classified. Only species included with significant and high indicator value ($IV \geq 20$) of the Indicator Species Analyses (see below) were included in the figure. Displaying the cumulative frequency of species for each vegetation type. For the comparison of Siberian birch forests and grasslands regarding to their share of forest and non-forest species, a Central European classification was used (Schmidt et al. 2011). The following groups were used: “Closed forest”; “Open forest” – forest edges, clearings; “Indifferent” – species occur both in forest and in open ecosystems; “Predominantly open areas, also forest” and “Open”. Finally the differences between European classification and the data collected in Siberia were calculated. The shifts “from open to forest habitats”, “from indifferent to forest habitats” and “from forest or indifferent to open habitats” were counted in case that the frequency in one of the Siberian habitats was zero. The shifts “from open or forest to indifferent habitats” were counted in case of that the species had in each of the habitats a frequency ≥ 8 .

The DCA was performed with Canoco 4.51 (Braak & Smilauer o.d.). The Indicator Species Analysis and Cluster analysis were conducted with PC-Ord 5 (McCune & Mefford 2006). The LM was calculated with R 2.13.1 (R Development Core Team 2010). All other calculations were computed with SPSS statistics 20 (IBM Corporations 2011). Data input was done with TurboVeg for windows 2.95 (Hennekens 2012). The map was created with ArcMap 10.0 (ESRI n.d.). For Graphics Sigma Plot 11.0 (Systat Software 2008), R 2.13.1 (package “rsm”) and Inkscape (Free Software Foundation 1991) were used.

Results

Siberian birch forest

Phytosociological overview

The analysed forests roughly fit in the phytosociological classification of Ermakov et al. (2000) (see Appendix b). Thirty-nine of the plots were related to the class Brachypodio pinnati-Betuletea pendulae. Delimitation was mainly carried out by the diagnostic species (DS) *Rubus saxatilis*, *Pulmonaria mollis*, *Vicia sepium* and *Angelica sylvestris*. The species *Kadenia dubia* (*Cnidium dubium*), *Heracleum sibiricum* and *Calamagrostis epigeios* defined the order Calamagrostio epigei-Betuletalia pendulae. These samples split into two alliances – Peucedano morisonii-Betulion pendulae, with *Fragaria viridis*, *Filipendula vulgaris*, *Phlomis tuberosa* and *Polygonatum odoratum* as DS and Calamagrostio epigei-Betulion pendulae with *Filipendula ulmaria* and *Lysimachia vulgaris* as DS. Using *Calamagrostis canescens* we separated one association – Phalaroido-Betuletum pendulae – from the second alliance. A complete list of species and synonyms is given in Appendix c.

Differences between forest types

In total we recorded 186 different plant species in all forest plots with an average of 27 species per plot and a maximum of 44 species.

Cluster analyses created four forest types: the extremes “dry” and “wet” as well as the intermediate moisture types “mesic open” and “mesic closed”. Environmental and structural comparison showed clear differences between these types (Tab. 1). The groups reflected two strong gradients: humidity and light. The “dry” forests were characterised by the lowest Ellenberg’s indicator value of humidity and nutrients. This type featured the highest trees while the height of herbs and the covers of shrubs and tree layer 2 were the lowest. Besides the forest type “mesic open” this type had the highest species richness. Located on the other side of the gradient was the forest type “wet” – with opposed characteristics: it showed the highest Ellenberg’s indicator value of humidity and nutrients, but the smallest trees (tree layer 1) and the highest herbs and established the lowest grade of species richness. There were similarities to the previous forest type – namely structural ones like the low covers from tree layer 2 and shrubs. The two mesic groups “open” and “closed” represented a lightness gradient. The “closed” type was highly influenced by a big cover of shrubs and tree layer 2. Light adapted species were fewer in this forest type while the “mesic open” forests showed the highest of all light indicator value for forest types. Moreover, here we found the highest number of species. Both types had mesic conditions and a medial indicator value of nitrogen.

In all types, most of the environmental parameters did not show significant differences. This concerned pH, conductivity, biomass of the field layer and amount of coarse woody debris.

Tab. 1: Mean and standard error of structural and environmental parameters of the forest types. Different letters indicate significant differences in means ($p < 0.05$) found by parametric Tukey test (A, B, C) or non-parametric Dunn's Method (a, b, c). * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, n.s. = not significant**

Forest Type	dry		mesic open		mesic closed		wet		
N	23		17		6		14		
mean ± standard error									P
Cover [%]									
Tree layer 1	48.0 ± 4.0		39.0 ± 5.4		49.0 ± 3.0		52.0 ± 6.6		<i>n.s.</i>
Tree layer 2	0.2 ± 0.1	a	4.0 ± 1.8	b	6.0 ± 4.8	a,b	2.0 ± 0.6	a,b	***
Shrub	5.0 ± 2.4	a,b	3.0 ± 1.3	a,b	20.0 ± 8.8	b	2.0 ± 1.8	a	*
Herbs	51.0 ± 4.1		60.0 ± 4.9		53.0 ± 8.2		67.0 ± 5.5		<i>n.s.</i>
Height [m]									
Tree layer 1	21.0 ± 0.6	A	19.0 ± 0.9	A,B	21.0 ± 0.8	A,B	17.0 ± 0.8	B	**
Tree layer 2	5.0 ± 3.0		8.3 ± 1.2		8.0 ± 1.5		8.0 ± 0.8		<i>n.s.</i>
Shrub	1.7 ± 0.1		1.6 ± 0.1		2.2 ± 0.3		2.0 ± 0.8		<i>n.s.</i>
Herbs	0.4 ± 0.0	A	0.5 ± 0.0	A	0.4 ± 0.1	A	0.7 ± 0.1	B	***
Environmental parameters									
pH	6.0 ± 0.2		6.6 ± 0.2		6.0 ± 0.6		6.4 ± 0.2		<i>n.s.</i>
Conductivity	208 ± 38.6		254 ± 54.6		478 ± 136.3		176 ± 25.4		<i>n.s.</i>
Biomass Field Layer	47.3 ± 3.8		53.5 ± 7.0		39.0 ± 5.5		58.0 ± 8.0		<i>n.s.</i>
Coarse Woody Debris	3.0 ± 1.1		3.4 ± 0.8		1.7 ± 0.7		4.1 ± 1.4		<i>n.s.</i>
Species Richness	30.3 ± 1.4	A	33.8 ± 1.5	A	28.2 ± 3.0	A,B	20.7 ± 2.0	B	***
Ellenberg's indicator value									
Light	6.4 ± 0.0	a	6.8 ± 0.0	b	6.2 ± 0.2	a	6.7 ± 0.1	a,b	***
Humidity	5.3 ± 0.1	a	5.9 ± 0.1	b,c	6.1 ± 0.2	a,b,c	7.0 ± 0.2	c	***
Nutrients	3.8 ± 0.1	a	4.4 ± 0.1	b	4.3 ± 0.2	a,b	5.2 ± 0.2	b	***

Indicator Species Analysis

Occasionally, relative frequencies differed not that much between the groups but indicator species analyses, including also abundance, distinguished the four forest types in a further way (Tab. 2). The “dry” forests delimited strongest with the indicator species *Calamagrostis arundinacea* and *Pimpinella saxifraga* (IV ≥ 50). The two species *Dracocephalum ruyschiana* and *Veronica teucrium*, both dryness indicator and only detected in these forests, gave further evidence for classification as “dry” forests. The indicator species *Hieracium umbellatum* and *Brachypodium pinnatum* occurred just in connection to the “mesic open” group. The “wet” type showed the highest indicator values – the first three all demonstrated values above 60 showing a strong affinity to this forest type. The type was represented by moisture and wetness indicators *Calamagrostis canescens*, *Stachys palustris*, and *Phragmites australis* (IV ≥ 50), consistent with the structural and environmental parameters. The indicator species of the “mesic open” forest were headed by *Galium boreale*, *Elytrigia repens*, *Phlomoidea tuberosa*, and *Serratula coronata*, whereas *Phlomoidea tuberosa* together with *Achillea millefolium*, *Artemisia lactiniata*, and *Galium verum* were just connected to “open” forests. “Mesic closed” forests were dominated by *Maianthemum bifolium*, *Equisetum pratense*, and *Angelica sylvestris* (IV ≥ 50). This forest type had no species occurring as a unique feature but some species are only found in one other forest type, namely “open” forests: *Viburnum opulus* and *Pulsatilla patens*.

Tab. 2: Indicator species analysis for the forest types. For each species, the percentage frequency within the corresponding type is given. The first column (IV) shows the maximum indicator value (grey shaded columns) over all types. In the delimitative part (just one column is grey), species with non significant or low indicator value (IV ≤ 20) are not shown. Species with high indicator values (IV ≥ 50) are given in bold. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$**

Forest type			dry	mesic open	mesic closed	wet
n			23	17	6	14
	IV	p	relative frequency/ abundance			
<i>Calamagrostis arundinacea</i>	61.7	*	70 / 89	18 / 4	50 / 7	7 / .
<i>Pimpinella saxifraga</i>	57	**	87 / 66	29 / 14	33 / 14	14 / 7
<i>Solidago virgaurea</i>	46.6	**	57 / 82	6 / 6	17 / 4	7 / 8
<i>Filipendula vulgaris</i>	39.6	*	61 / 65	35 / 20	17 / 15	. / .
<i>Agrimonia pilosa</i>	39.6	**	57 / 70	24 / 7	50 / 20	7 / 2
<i>Hieracium umbellatum</i>	39.5	**	52 / 76	24 / 16	. / .	7 / 8
<i>Polygonatum odoratum</i>	36.4	*	48 / 76	12 / 2	17 / 20	7 / 2
<i>Trifolium medium</i>	34.5	**	43 / 79	6 / 9	17 / 12	. / .
<i>Brachypodium pinnatum</i>	32.8	*	48 / 69	29 / 31	. / .	. / .
<i>Dracocephalum ruyschiana</i>	30.4	**	30 / 100	. / .	. / .	. / .
<i>Veronica teucrium</i>	25.1	**	26 / 96	. / .	. / .	7 / 4
<i>Galium boreale</i>	69.9	*	96 / 17	100 / 70	83 / 11	21 / 2
<i>Elytrigia repens</i>	59.8	*	43 / 16	82 / 73	50 / 6	21 / 5
<i>Phlomoidea tuberosa</i>	52.8	*	35 / 31	76 / 69	. / .	. / .
<i>Serratula coronata</i>	51.1	*	22 / 12	65 / 79	17 / 9	. / .
<i>Vicia cracca</i>	48.5	*	30 / 16	82 / 59	50 / 11	43 / 15
<i>Calamagrostis epigeios</i>	47.2	*	17 / 15	65 / 73	. / .	7 / 12
<i>Rosa majalis</i>	47.2	***	48 / 14	94 / 50	50 / 23	43 / 13
<i>Achillea millefolium</i>	45.7	***	48 / 29	65 / 71	. / .	. / .
<i>Inula salicina</i>	43.6	*	57 / 29	88 / 49	33 / 18	14 / 5

<i>Lactuca sibirica</i>	40.5	**	. / .	47 / 86	. / .	7 / 14
<i>Artemisia laciniata</i>	37.6	*	13 / 9	41 / 91	. / .	. / .
<i>Veronica longifolia</i>	32	***	13 / 9	71 / 45	33 / 34	29 / 12
<i>Heracleum sphondylium</i>	31.2	*	43 / 31	53 / 59	17 / 10	. / .
<i>Poa pratensis</i>	30.1	**	4 / 10	41 / 73	17 / 12	7 / 5
<i>Galium verum</i>	26.7	**	17 / 24	35 / 76	. / .	. / .
<i>Asparagus officinalis</i>	23.5	*	. / .	24 / 100	. / .	. / .
<i>Maianthemum bifolium</i>	59.7	**	22 / 8	. / .	67 / 90	7 / 3
<i>Equisetum pratense</i>	52.5	**	65 / 20	18 / 1	67 / 79	7 / 1
<i>Angelica sylvestris</i>	52.1	*	39 / 11	76 / 10	67 / 78	14 / 2
<i>Sorbus aucuparia</i>	49.1	***	4 / 2	. / .	50 / 98	. / .
<i>Viburnum opulus</i>	42.6	*	9 / 15	. / .	50 / 85	. / .
<i>Frangula alnus</i>	27.1	**	4 / 7	. / .	33 / 81	7 / 12
<i>Pulsatilla patens</i>	24.7	*	17 / 26	. / .	33 / 74	. / .
<i>Calamagrostis canescens</i>	74	*	39 / 7	65 / 13	33 / .	93 / 80
<i>Cirsium arvense</i>	67.5	**	22 / 2	59 / 9	67 / 9	86 / 79
<i>Stachys palustris</i>	63.9	*	. / .	35 / 7	17 / 4	71 / 89
<i>Phragmites australis</i>	56.3	*	13 / 2	12 / 11	. / .	64 / 88
<i>Lysimachia vulgaris</i>	49.8	***	30 / 4	88 / 23	67 / 9	79 / 63
<i>Dryopteris carthusiana</i>	29.3	**	4 / 2	6 / 6	17 / 9	36 / 82
<i>Galium aparine</i>	29.2	***	. / .	. / .	33 / 32	43 / 68
<i>Lycopus europaeus</i>	26.5	*	4 / 1	6 / 6	. / .	29 / 93
<i>Solanum dulcamara</i>	26.3	*	4 / 8	. / .	. / .	29 / 92
<i>Ranunculus lingua</i>	21.4	*	. / .	. / .	. / .	21 / 100
dominant species (frequency ≥ 20 in each forest type)						
<i>Betula pendula</i>	31.3	0.15	100 / 25	100 / 20	100 / 24	100 / 31
<i>Rubus saxatilis</i>	35.7	0.09	87 / 29	94 / 38	83 / 20	57 / 14
<i>Pulmonaria mollis</i>	51.9	0.49	78 / 66	94 / 12	100 / 20	21 / 1
<i>Kadenia dubia</i>	25.5	0.61	74 / 19	76 / 27	67 / 18	71 / 36
<i>Filipendula ulmaria</i>	34.7	0.22	35 / 4	94 / 23	83 / 42	50 / 31

Ordination

The DCA revealed a strong environmental gradient associated with the first axis, running from humid, nutrient-rich areas (sample scores $\geq |-0.8|$, $P = ***$), where the “wet” forest type was located to the dryer areas, represented by “dry” forests (Fig. 2). Moreover, the sample scores of the first axis depicted a negatively significant correlation with the Ellenberg’s indicator value for light and the height of herb layer (Tab. 3). The species richness and the height of tree layer 1 were opposed to this positively correlated with this axis. The second axis displayed mainly the light conditions of the sites (sample score Ellenberg light -0.75 , $P = ***$). These conditions were determined by the significantly correlated structural parameters as cover herbs (negative), cover tree 1 and cover shrub (positive). Conductivity, height of the shrub layer, and cover of tree layer 2 did not show significant correlation to the first two axes. The two mesic forest types were distributed over this gradient with low variance regarding to the first axis. “Dry” forest showed quite a wide spread regarding to the second axis.

With an Eigenvalue of 0.333, the first axis of the DCA explained 11.8 % of the total inertia of the species data. The second axis explained 6 % with an Eigenvalue of 0.161.

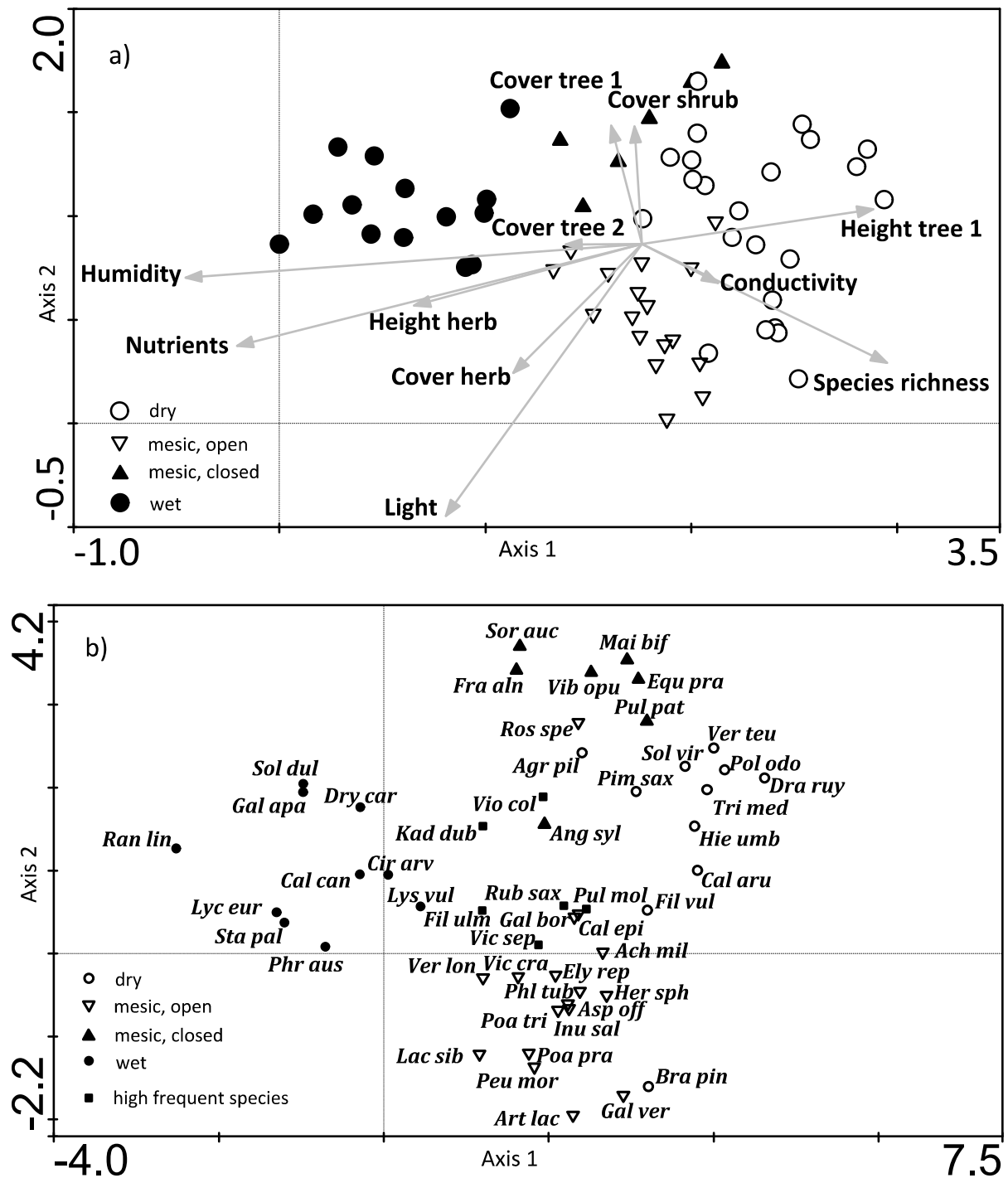


Fig. 2: Detrended Correspondence Analysis (DCA) of birch forest vegetation data (percent cover by species). a) samples – each symbol represents another forest type (defined by the cluster analyses) and overlay of structural and environmental parameters, b) significant indicator species of the Indicator Species Analysis and high frequent species (frequency > 15 in each of the forest types).

Tab. 3: Spearman rank correlations between the first two DCA axes and a subset of environmental variables. Only variables with $r_s \geq |0.1|$ for at least one axis are shown. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, n.s. = not significant**

	Axis		Axis	
	1	P	2	P
Eigenvalue	0.33		0.16	
Ellenberg Humidity	-0.93	***	0.00	n.s.
Ellenberg Nutrients	-0.80	***	-0.20	n.s.
Species richness	0.55	***	-0.40	**
Height herb	-0.53	***	-0.05	n.s.
Height Tree1	0.50	***	0.05	n.s.
Light	-0.36	**	-0.75	***
Cover tree 1	-0.07	n.s.	0.33	**
Cover herb	-0.22	n.s.	-0.29	*
Cover shrub	0.00	n.s.	0.30	*

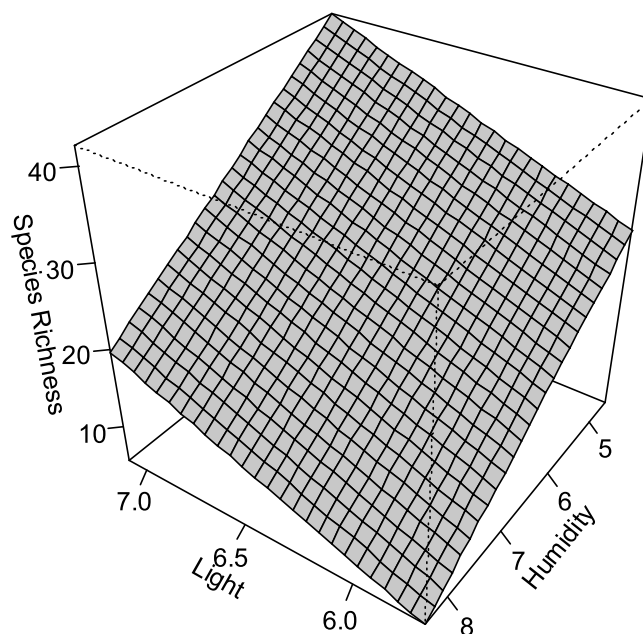


Fig. 3: Statistics of LM (Linear Model): Response of species richness to Ellenberg's indicator values for Light and Humidity. Tested with several environmental parameters (predictor variables) – non-significant predictors were excluded from the final model by stepwise backward-selection ($P > 0.05$). $R^2 = 0.3896$

Species Richness

In all forest plots, the Ellenberg's indicator values for light and humidity were significant predictors of overall species richness. Both parameters operated inversely – low humidity and high light values led to high species richness (Fig. 3). Humidity acted in a range of 4.6 (min.) to 8.4 (max.) and was on average 5.9. Light showed a more narrow range from 5.7 to 7.1 with a mean of 6.6.

Forest and Grassland

Indicator species analyses

On all plots we could find a total of 289 vascular plants which were composed of 186 species in forests and 201 in grasslands. *Galium boreale*, *Kadenia dubia*, *Filipendula ulmaria*, and *Lathyrus pratensis* were overall dominant species, occurring equally in both vegetation types (Tab. 4). The Indicator species analyses detected 26 significant indicator species (IS) of forests and 31 significant IS of grasslands. 12 IS of the forest did not appear in the grasslands and vice versa: 5 of the grassland IS did not grow in the forests. In the forests, species with the highest indicator value (IV) were *Rubus saxatilis*, *Pumunaria mollis*, *Calamagrostis canescens*, and *Rosa majalis*. In the grasslands, *Poa angustifolia*, *Potentilla argentea*, *Galium verum*, and *Achillea millefolium* were the species with the highest IV.

Tab. 4: Indicator species analysis for the structural vegetation types forest and grassland (ecosystem). For each species the percentage frequency within the corresponding type is given. The first column (IV) shows the maximum indicator value (grey shaded columns) over both types. Except in the part of the dominant species, species with non significant or low indicator value (IV < 20) are not shown. Species with high indicator values (IV ≥ 50) are given in bold. * = p < 0.05, ** = p < 0.01, *** = p < 0.001

Ecosystem			Forest	Grassland
N			62	67
	IV	p	relative frequency/ abundance	
<i>Rubus saxatilis</i>	79.3	***	79 / 100	3 / .
<i>Pulmonaria mollis</i>	71.3	***	71 / 100	6 / .
<i>Calamagrostis canescens</i>	58.7	***	59 / 100	. / .
<i>Rosa majalis</i>	57	***	59 / 97	17 / 3
<i>Lysimachia vulgaris</i>	49.3	***	60 / 82	11 / 18
<i>Angelica sylvestris</i>	44.4	***	44 / 100	. / .
<i>Geranium pseudosibiricum et Pratense</i>	42.5	***	49 / 86	15 / 14
<i>Populus tremula</i>	39.7	***	40 / 100	. / .
<i>Calamagrostis arundinacea</i>	38.1	***	38 / 100	. / .
<i>Vicia sepium</i>	36.7	**	57 / 64	21 / 36
<i>Agrimonia pilosa</i>	36.5	***	37 / 100	. / .
<i>Equisetum pratense</i>	36.5	***	37 / 100	. / .
<i>Inula salicina</i>	34.2	**	52 / 65	11 / 35
<i>Heracleum sphondylium</i>	30.8	***	34 / 92	6 / 8
<i>Serratula coronata</i>	27.5	**	30 / 91	12 / 9
<i>Brachypodium pinnatum</i>	27	***	27 / 100	. / .
<i>Lathyrus pisiiformis</i>	26.7	***	27 / 99	3 / 1
<i>Hieracium umbellatum</i>	26.5	***	27 / 98	6 / 2
<i>Orthilia secunda</i>	25.4	***	25 / 100	. / .
<i>Polygonatum odoratum</i>	25.4	***	25 / 100	. / .
<i>Solidago virgaurea</i>	25.4	***	25 / 100	. / .
<i>Viola collina</i>	25.4	***	25 / 100	. / .
<i>Stachys palustris</i>	24.7	***	27 / 91	3 / 9
<i>Moehringia lateriflora</i>	23.6	***	24 / 99	2 / 1
<i>Carex acutiformis</i>	23.3	***	24 / 98	6 / 2
<i>Phragmites australis</i>	22.2	***	22 / 100	. / .
<i>Poa angustifolia</i>	90.1	***	5 / 1	91 / 99
<i>Potentilla argentea</i>	65	***	3 / 3	67 / 97
<i>Galium verum</i>	62.5	***	16 / 6	67 / 94
<i>Achillea millefolium</i>	62.1	***	37 / 7	67 / 93
<i>Festuca rupicola</i>	61.7	***	8 / 1	62 / 99
<i>Taraxacum officinale</i>	60.6	***	16 / 5	64 / 95
<i>Veronica spicata</i>	51.5	***	. / .	52 / 100
<i>Stellaria graminea</i>	45.5	***	. / .	45 / 100
<i>Elytrigia repens</i>	43.1	**	49 / 21	55 / 79
<i>Carex praecox</i>	42.9	***	8 / 12	48 / 88
<i>Vicia cracca</i>	42.8	*	48 / 28	59 / 72
<i>Phleum phleoides</i>	41.8	***	2 / 1	42 / 99
<i>Astragalus danicus</i>	37.9	***	. / .	38 / 100

<i>Ranunculus acris</i>	37.9	***	8 / 17	45 / 83
<i>Filipendula vulgaris</i>	37.9	**	35 / 4	39 / 96
<i>Fragaria viridis</i>	36.8	**	37 / 19	45 / 81
<i>Plantago media</i>	35.8	***	3 / 2	36 / 98
<i>Potentilla anserina</i>	33.6	***	5 / 3	35 / 97
<i>Agrostis tenuis</i>	32.8	***	3 / 2	33 / 98
<i>Artemisia austriaca</i>	31.2	***	2 / 2	32 / 98
<i>Bromopsis inermis</i>	29.4	***	8 / 3	30 / 97
<i>Seseli libanotis</i>	28.3	***	5 / 2	29 / 98
<i>Plantago maxima</i>	25	***	5 / 3	26 / 97
<i>Peucedanum morisonii</i>	24.6	***	5 / 10	27 / 90
<i>Carex tomentosa</i>	24.2	***	. / .	24 / 100
<i>Trifolium pratense</i>	24	**	10 / 12	27 / 88
<i>Galatella biflora</i>	22.9	**	8 / 5	24 / 95
<i>Melampyrum cristatum</i>	22.4	**	5 / 8	24 / 92
<i>Alopecurus pratensis</i>	22.3	***	2 / 2	23 / 98
<i>Myosotis ramosissima</i>	21.2	***	. / .	21 / 100
<i>Glechoma hederacea</i>	20.1	**	8 / 12	23 / 88
dominant species (frequency ≥ 20 in each Ecosystem)				
<i>Galium boreale</i>	34.5	0.64	78 / 44	47 / 56
<i>Kadenia dubia</i>	35.2	0.46	73 / 23	45 / 77
<i>Filipendula ulmaria</i>	26.6	0.99	59 / 45	48 / 55
<i>Lathyrus pratensis</i>	35.1	0.06	43 / 25	47 / 75
<i>Cirsium arvense</i>	33.6	0.16	49 / 68	32 / 32
<i>Pimpinella saxifraga</i>	22.3	0.70	48 / 30	32 / 70
<i>Phlomoideis tuberosa</i>	25.7	0.14	35 / 19	32 / 81
<i>Sanguisorba officinalis</i>	18.9	0.62	37 / 34	29 / 66
<i>Calamagrostis epigeios</i>	18	0.38	25 / 41	30 / 59

Siberia and Europe

A comparison of species of Siberian forests and grasslands with the European classification of Oberdorfer (2000) as a base showed clear differences (Fig. 4). The forests were dominated by forest species but closely followed by wet grassland species. The share of dry grassland species had a middle position while near forest and ruderal species occurred least of all. The grassland delimited distinctly from forest. This vegetation type was dominated by far by dry grassland species. Ruderal species take second place. Species of wet grasslands, near forest habitats, and forests played but a minor part.

The second comparison had a stronger focus on forest and non-forest species and detected also some differences (Fig. 5). Species which can be found in Central Europe in forests as well as in open areas clearly dominated forests here. All others appeared equally in forests, open, and predominantly open areas. Species of open forest almost did not occur. There were no forest species at all in grasslands and only a neglectable share of species of open forest. Species of open and predominantly open areas, followed by indifferent ones, were here the dominant species.

To point out differences between the habitat requirements of the same species in Europe and Siberia, we counted shifts of habitats (Tab. 5). Ten of the species grew in Europe in forests as

well as in open habitats; in Siberia we found them only in forests. Seven of the species which grow in Europe in forests or in open areas showed indifferent behaviour in Siberia. We also found strong contrasts: three species which occur in Europe strictly in open habitats were found here in forest plots only. One species – *Carex tomentosa* – classified in Europe as forest or indifferent species was detected by us only in grasslands during this study.

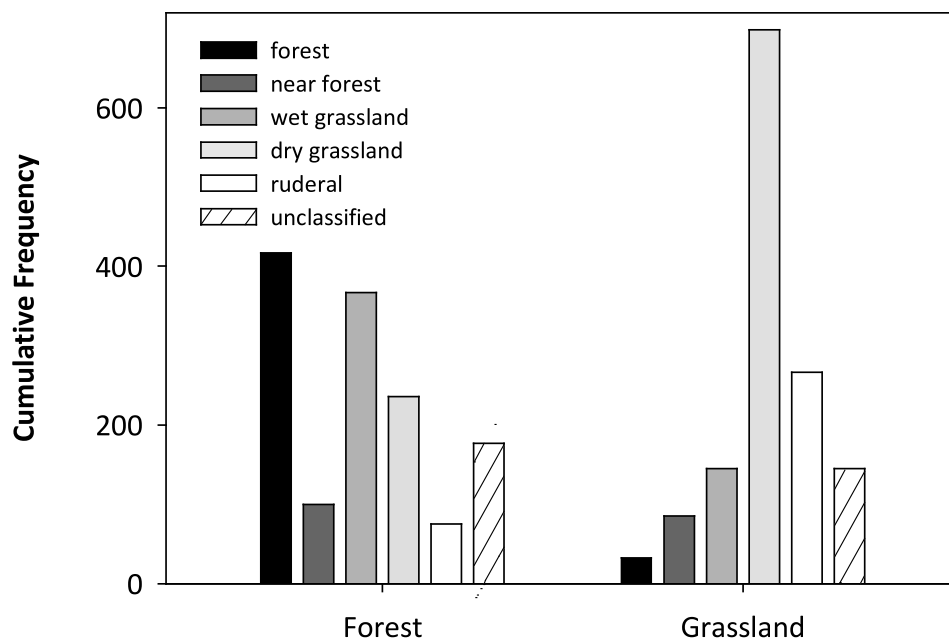


Fig. 4: Comparison of European habitat preferences in Siberian forests and grasslands. Bars display cumulative frequency of species from both vegetations types, based on a central European classification (Oberdorfer 2000). All species included with significant and high indicator value ($IV \geq 20$) of the Indicator Species Analyses. For some species, a classification was not possible (unclassified). Forest N = 63; Grassland N = 66

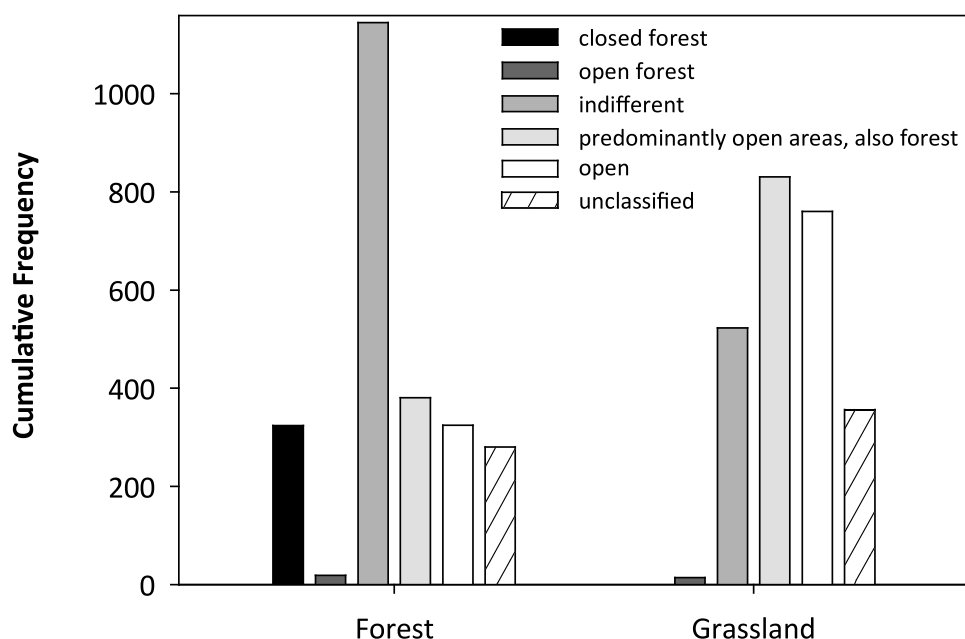


Fig. 5: Comparison of Siberian birch forests and grasslands regarding to their share of forest and non-forest species. Bars display Cumulative frequency of species with frequency > 5, based on a Central European classification (Schmidt et al. 2011). The indifferent species appear both, in forests and in open areas. For some species a classification was not possible (unclassified). Forest N = 63; Grassland N = 66

Tab. 5: Comparison of European forest species classification (Schmidt et al. 2011) and self sampled data in forests and grasslands of Siberia. Displayed are the numbers of changes between these two classifications. Forest N = 63; Grassland N = 66

Species of				
Europe	open habitats	indifferent habitats	forest or indifferent habitats	open or forest habitats
Shift to				
Siberia	forest habitats	forest habitats	open habitats	indifferent habitats
	3	10	1	7
no changes: 55; unclassified: 25				

Discussion

Ellenberg's indicator values

Although it is controversial to use **Ellenberg's indicator values** outside from central Europe, we decided to use them in this study because of the following. We could identify clear differences between plots as related to the values. The theory of the relative constancy of habitat (Walter 1953) gave us, in our opinion, legitimation to do so. Although many observed plants grow in Siberia, judged from a European point of view, at atypical sites, they still have the same requirements of their environment and indicate specific conditions. A good example is *Veronica teucrium*. Its principal occurrence is specified in central Europe as semi-dry grassland. The plant has a light indicator value of seven. In our plots it occurred on dry forest sites. At these sites, the habitat requirements of the species are met because the site characteristics are similar to Mid-European dry grassland. Previous studies showed that that the use of Ellenberg's indicator values is also possible outside of Central Europe: values are already used in northern (e.g. Persson 1981, Diekmann 1994, Lawesson 2000) and eastern Europe (Prieditis 1997, Ruprecht & Botta-Dukat 2000).

Of course the outcomes of non-European relevés are not comparable with values of European relevés. In this study, we only compare values of relevés of the same region in between each other. We could show that there are differences between our plots regarding to humidity, light and nutrient condition. However, we cannot evaluate the range of each value without consideration other information. This is what we aim for later in this discussion.

Characteristics of Siberian birch forest

Species inventory as well as environmental and structural parameters visualise the detailed characteristics of Siberian birch forests. Not surprisingly, light and humidity were identified as the most important determinants for the species richness. Chytrý (2010) also detected canopy shading in the southern Urals, which is directly influencing the light conditions, as the distinctive factor for species richness. However he studied this relation in a greater contrast, comparing birch forest with 40 – 50 species per plot with shaded *Acer*, *Tilia* and *Ulmus* forest with usually 12 – 20 species. In eastern Siberia in the Altai, Chytrý 2012 also found the vegetation richest in species in forests with an open canopy cover. In those forests, light-demanding species,

characteristic of tall-grass steppes and mesic to wet meadows, were favoured. Indeed, in our study as well as in the study in the Altai, the high species richness of the forests was related to their rich herb layer, whereas there were just a few species of trees and shrubs. As an approval, our “mesic open” forest type showed the highest species richness by reason of low tree and shrub cover. Additionally, most light demanding species occurred in this forest type. Moreover, species richness increased with humidity. This indicates that dryness was a stress factor which led to lower species richness. Wetness however, acting in a mesic range had no stressing effect and led to higher species numbers. This could be a consequence of the forest habitat, moderating extremes of the continental macroclimate of the wider open area (Chytrý 2012).

Due to its strong influence, light and humidity were also the two determining factors for delimitation of the four forest types. Closely related to these factors are the structural parameters. The forest type “**mesic closed**” consisted of a small sample size (6 samples) but these few samples clearly deviated from the other groups that’s why we did not disperse the group. For this reason, however, a few parameters did not differentiate significantly from other groups but still showed strong tendencies. One main point is the high grade of structures due to high tree and shrub cover. This results in very dark sites. The type is botanically characterised on one hand by mesic forest species as *Maianthemum bifolium* or *Sorbus aucuparia*, on the other hand by species of moist habitats as alluvial forests and wet grassland represented by *Frangula alnus*, *Viburnum opulus*, *Equisetum pratense* and *Angelica sylvestris* (Oberdorfer 2001). Compared with the “wet” forests, these forests were still classified as mesic. This is, among other factors, due to the occurrence of *Pulsatilla patens* which also was one of the indicator species of this forest type. The plant’s habitat requirements are intermediate light dry sites (Sebald et al. 1993).

To some extent, we found opposite conditions in the “**mesic open**” forest type. In these forests, lower cover of trees and shrubs were typical. Already on site the plots seemed to be more open and sunny (see Appendix a). What is more, the cover of herbs was the lowest in these forests. All these factors supported the development of high species diversity. Because dominant species were missing, less competitive species could establish (Grime 1973). Thus, the “mesic open” forests showed parallels to open grassland vegetation which we find in central Europe. A view on the species can confirm this assumption. Several indicator species are known from open habitats, for example *Vicia cracca*, *Achillea millefolium*, *Inula salicina*, *Veronica longifolia*, *Poa pratensis*, *Elytrigia repens*, and *Galium verum* (Oberdorfer 2001). Furthermore, *Phlomis tuberosa* should be mentioned as a typical species from steppes. *Artemisia laciniata*, known as a salt-tolerant species in central Europe, shows in its native region – continentally central Asia – a distribution in open birch and poplar forests (Fischer et al. 2008). Because of its good adaption to the continental climate of Siberia, it is a strong competitor. In the milder climate of central Europe, it is restricted to extreme habitats as salty soils due to better adapted competitors. This type seems to be the most typical one of the open birch forest which mainly constitutes the forest steppe. The species inventory and the environmental parameters showed a combination of steppe and forest.

Beside the gradient of shade, there is a second one along the humidity gradient where two more types delimited from each other: “wet” and “dry”. The “**wet**” forests had the highest herb layer. This can easily be explained by high growing species as *Phragmites australis*, which were dominant in these forests as well as by the favourable growing conditions for plants. In these plots we had highest indicator value for nutrients. These sites supported a couple of species with sufficient resources to enable them to become dominant and suppress other, less competitive species (Grime 1973, Ellenberg & Leuschner 2010). Consistent with this finding, we found the lowest species richness in these plots. Many of the indicator species are inhabitants of wet or wet-dry

sites in central Europe. *Calamagrostis canescens* grows in humid to wet forests, e.g. Alder carr woodlands, but it can partly infringe on clearings and meadows. With its high competitiveness and water demand for germination of seeds, *Phragmites australis* is a well known dominant wetland species (Sebald et al. 1998). Although the plots seemed to be rather dry in the sampling period, observations in spring showed waterlogging at many sites. We conclude that this period of time might be crucial for the species inventory. *Solanum dulcamara*, *Stachys palustris* and *Ranunculus lingua* are characteristic for wet as well as nutrient rich sites. One exception of the humidity loving IS is *Cirsium arvense*. It is a representative for nutrient adapted species typically growing at croplands and nutrient rich sites (Oberdorfer 2001). In the “dry” forest type, *Polygonatum odoratum*, *Pimpinella saxifrage*, and *Dracocephalum ruyschiana* are IS. These are species of moderately dry habitats and therefore confirm the picture of a dry forest (Sebald et al. 1992 & 1996). Some species are not specialised in life in dry habitats, occurring in both in dry and humid areas. These are represented by *Filipendula vulgaris*, *Hieracium umbellatum*, and *Solidago virgaurea*. Similar to its European relative *Agrimonia eupatoria*, *Agrimonia pilosa* inhabits mesic sites (Plantarium n.d.). Lastly, *Brachypodium pinnatum* should be mentioned. It is growing in central Europe usually at semi-dry grassland and seldom in open forests and is favoured by fire.

Fire was in all types a recurrent phenomenon. Its marks on the stems of the birches as well as recently burned sites are evidence of a high fire frequency. Fire as an important ecological factor controls both environments for vegetation establishment and vegetation succession. It therefore determines structure and productivity of the forests (Abaimov & Sofronov 1996). Studying how fire frequency is related to diversity patterns in this specific area is an interesting study object for future research, for example by using dendro chronology, but could not be considered in this study.

Discussing the difference between the created forest types, things they have in common should also be mentioned. Beside *Betula pendula* – *Rubus saxatilis*, *Pulmonaria mollis*, *Kadenia dubia* (*Cnidium dubium*), and *Filipendula ulmaria* were also represented in all types. The last two both grow on wet and partly waterlogged sites. *R. Saxatilis* and *P. mollis* grow, by contrast, on mesic sites. The gradient shown by the species, extends from mesic to wet sites but dry sites are absent. Within the humid sites, the species composition indicates a highly variable moisture regime. These observations correspond to the circumstance discussed above that dryness acted as a stress factor, while wetness acted in a mesic range instead. Both give hints at which wetness scale we should “measure” the forests. As discussed in the beginning, the Ellenberg’s indicator value for humidity gives relative information but no range of the value. This could be approximated by these species and environmental information.

Forest and Grassland

An analysis of the species composition of both forest and grassland provides a lot of synergetic information about their habitats and its foregone development.

Ermakov et al. (2000) state that the main part of the species inventory in the **hemiboreal forest** is formed by species which are not true forest plants. They are rather “forest-grassland, forest-steppe, meadow-steppe species” (Ermakov et al. 2000: 5). In this study, we primarily used central European classification to understand and classify the species inventory. So from European point of view we endorse Ermakov. Beside a base of typical forest species, our forests showed a high amount of open landscape species, represented by wet grassland and also a smaller amount of dry grassland and ruderal species. IS *Inula salicina* can serve as an example: it is a typical plant of open

habitats, primarily growing on wet meadows (Oberdorfer 2001). Also *Anemone sylvestris* and *Potentilla erecta* should be mentioned, although they are not IS: In central Europe, these species are known as species with a particular emphasis on open habitat and just a minor presence in forests (Schmidt et al. 2011). Also, these species were completely missing on grasslands. There are several more species, also among the IS, showing the same pattern. This concerns e.g. *Brachypodium pinnatum* or *Phragmites australis*. The biggest part of the species inventory was composed of “indifferent” species. They have no emphasis on open or closed habitats. Some examples are *Solidago virgaurea*, *Hieracium umbellatum*, *Carex acutiformis*, *Lysimachia vulgaris*, *Inula salicina* or *Angelica sylvestris* (Schmidt et al. 2011). The mixture of species, especially of those growing typically on mesic and wet sites and even some on dry sites, approves the wide range and variability of the moisture regime in our forests. As mentioned above, we still observed a base of forest species. The four main indicator species are typical for forest habitats. Ahead *Rubus saxatilis*, preferring summer warm dark coniferous and deciduous forest. We also detected it at some grassland plots but its numbers were marginal. Species as *Equisetum pratense*, *Orthilia secunda*, *Polygonatum odoratum*, and *Viola collina* were also representatives of European forest species (Oberdorfer 2001). These we never detected at grassland sites. In general, many species we observed in forests were not found at grassland plots. It turns out, that however, most of the grassland species also occurred in the forest. This is consistent with the finding of Ermakov et al. (2000), who stated that the forest is a mixture of different influences and developed out of several different habitats including also grasslands. In the study of Nimis et al. (1994), likewise conducted in the west Siberian plain, open landscape communities as Molinio-Arrhenatheretea (moist meadows and pastures) Festuco-Brometea (more or less arid, poor calcareous grasslands), and Artemisietea (nitrophilous ruderal) also played an important role in the forests. In our case, however, species of Festuco-Brometea (sociological unit in this study of the group “dry grassland”) were predominantly found in grassland plots. The group “dry grassland” species made up by far the largest part of the **grasslands’ species inventory**. Some of the main IS as *Potentilla argentea*, *Festuca rupicola*, and *Galium verum* are deemed as such (Oberdorfer 2001). Moreover, ruderal species and species of wet grassland were found in the grasslands. Here, *Poa angustifolia*, *Elytrigia repens*, and *Glechoma hederacea*, occurring typically in ruderal grasslands, act as good examples for ruderal sites. As representative examples for the wet grasslands, *Achillea millefolium* and *Taraxacum officinale* can be mentioned (Oberdorfer 2001). Species known as inhabitants of dark forests were never detected. Species of open forests were also very scarce. In this point, the grasslands did not deviate from forest plots. This might be due to a different understanding of “open” or “steppe forest” in Europe and in Siberia. Nowadays, steppe forest of Europe is different from the one of the Pleistocene. The species grew socialised differently and under different environmental conditions (Ellenberg & Leuschner 2010). We get the same picture today, comparing current steppe forest of Europe and Siberia. The soil conditions differ much: While we find deep humous soils in Siberia, there are only shallow relicts of this in Europe. This leads to different conditions and thus to a different species inventory. Consequently, what in Europe are so called “open forest species” probably find their habitat apart open forests and grasslands in Siberia. This might be an explanation for the lack of open forest species in the plots. Some species showed no particular preference for one of the habitats. These are mainly *Galium boreale*, *Kadenia dubia*, *Filipendula ulmaria*, *Lathyrus pratensis*, and *Cirsium arvense*. They have in common that they all are species of open habitats – wet grasslands and ruderal sites. *Phlomis tuberosa* and *Calamagrostis epigeios* are two of just a few exceptions which have also a distribution in forests (Fischer et al. 2008).

In general, our forest seemed to be more heterogeneous in respect to the species composition as opposed to the more homogeneous grasslands. It is a complex composition of typical forest species and a fairly high amount of open landscape species as well as hosting species from dry and wet sites indicating a wide range of humidity. Consequently, it seems that from European point of view, there is a shift of open landscape species into the forest. This concerns species of humid and wet habitats, particularly. They do not find good conditions of growth “outside” in hot continental summer climate. In the open forest, they have better conditions: On one hand, it is temperature-controlled with less extreme temperatures and temperature changes and on the other hand, due to the open character of the forests, the plants still get enough light, but are also protected from transpiration (Hofmeister 2004). These species did not change their habitat requirements, but the habitats, where these could be found, changed. This is consistent with the theory of relative site constancy (Walter 1953). The heterogeneity of the forest is also explainable by the share of different phytogeographic origins. According to Nimis et al. (1994), in the forests Circumboreal-temperate species meet Eurasiatic species as well as Asiatic species. This mixture reflects the sensitivity of the subzone where also many species reach their distribution boundaries.

Modern Analogue

Is it permissible to use West Siberia Birch forest as modern analogues to Pre-Boreal European forests? The evidence suggests “yes”. Several studies proved a close connection of the European and Eurasian vegetation (Nimis et al. 1994, Kuneš et al. 2008, Chytrý 2008 & 2010). Nimis et al. 1994 stated that “most of the species presently occurring in the southern Siberian *Betula* stands have an Eurasiatic-temperate distribution.” (p. 37). So in general, there is a large overlap in fundamental species inventory. Furthermore, going back in history, it is noticeable that the southern part of the West Siberian Plain was never subjected to Pleistocene glaciations (Nimis et al. 1994). However, the climate also affected the sparse birch woodlands and it was partly displaced by southern forest-tundra. This, though, was later transformed into periglacial steppe vegetation with again sparse birch woodlands (Giterman et al. 1968, Borisova et al. 2011). Somehow, the Siberian birch stands could be considered as the last remnants of a temperate deciduous forest belt which was more widespread before glacier times and extended to Europe (Nimis et al. 1994). So, some of this temperate deciduous forest belt was able to partly survive in West Siberia and today can open a view back to the past of Europe.

The birch forests studied in this study represent one forest type (*Betula*-*Populus*) Chytrý (2010) observed in his study. Following Chytrý and his theory of European-Siberian analogues, we thereby observed one sequence, the oldest of European Holocene history. This period is assumed to have hosted a high richness of light-demanding species in the herb layer and being the origin of today’s species richness in open landscape (Chytrý et al. 2010). Also Nimis et al. (1994) stated that many birch woodland species are not part of the European forest flora, being most frequent in grassland, tall herb, and forest margin communities.

The discussion above already supported these theories in many ways. The numbers of the “shift table” are obvious: Three species which in Europe grow in open landscapes and ten which behave indifferent in Europe were found in our study in forests only. In Europe, the occurrence of indifferent species in the forests is closely related to the grade of canopy cover (Schmidt et al. 2011). The open character of the Siberian forest seems to offer most favourable growing conditions for these species. Then again, this could also mean that these species developed in

open early Holocene forests and nowadays grow in habitats which come closest to these previous habitats.

In summary our results give further evidence that Pre-Boreal open-canopy forests in Central Europe were rich in light-demanding species and therefore could have served as the origin of the flora of nowadays' open ecosystems.

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b) Diagnostic Species (D.S.) of samples referring to the classification of Ermakov et al. 2000.

Sample nr.	1	52	9	13	24	49	18	20	51	19	40	5	4	6	47	59	15	57	60	53	46	43	62	7	30	29	50	25	54	16	38	42	58	2	37	14	44	28	32						
D.S. Cl. Brachypodio pinnati-Betuletea pendulae																																													
Rubus saxatilis	1	2	2	2	r	3	3	3	3	2	1	3	2	4	3	2	2	2	2	2	.	2	3	2	.	3	2	2	2	4	2	3	3	2	2	2	2	2	3	3	2				
Pulmonaria mollis	r	r	r	r	r	r	r	r	r	.	r	r	r	r	r	+	.	r	+	r	+	r	2	+	r	2	+	r	+	r	.	5	.	r	2	+	r	r	r	r	r				
Angelica sylvestris	r	r	r	r	.	.	r	r	.	r	.	r	r	r	r	r	r	.	.	r	.	+	.	r	2	r	r	.	.	+	.	.	r	1	r	.	.	.	.	.	.				
Vicia sepium	r	r	r	+	r	r	r	r	r	r	r	r	r	.	r	r	r	.	r	r	.	2	r	+	r	.	.	r	.	.	r	.	r	r	.	.	.	.	r	r	r	r			
Calamagrostis arundinacea	2	.	.	.	.	.	.	.	.	3	.	2	.	.	.	.	.	2	.	.	.	3	2	.	3	2	.	3	2	.	r	3	.	3	2	3	2	1	r	+	4	2			
Brachypodium pinnatum	2	.	.	.	.	.	.	.	.	r	2	2	.	2	.	.	2	2	.	.	.	.	2	.	2	.	2	.	2	.	.	3	r	r	2	.	.	.	.	2	4				
Serratula coronata	1	+	r	.	r	r	r	.	.	r	r	r	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r		
Hieracium umbellatum	.	r	.	.	.	r	.	.	.	.	.	r	.	.	.	r	.	r	.	.	r	2	.	.	.	.	.	.	r	.	r	.	2	.	.	.	.	+	r	.	.				
Pleurospermum uralense	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.			
D.D. Ord. Calamagrostio epigei-Betuletalia pendulae																																													
Kadenia dubia	r	r	r	r	.	r	r	r	r	r	r	r	r	.	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r	.	r			
Heracleum sibiricum	.	.	.	.	.	r	.	.	.	r	.	.	.	r	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	r		
Calamagrostis epigejos	3	.	.	.	.	3	1	.	.	.	2	.	2	.	.	3	2	.	2	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
D.S. Ass. Peucedano morisonii-Betuletum pendulae = D.S. All. Peucedano morisonii-Betulion pendulae																																													
Fragaria viridis	r	.	.	r	.	.	.	.	.	1	.	.	.	.	.	2	.	r	r	r	+	r	r	.	r	.	r	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Filipendula vulgaris	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	r	r	r	r	r	.	r	.	r	.	r	.	r	r	r	r	r	r	r	r	.	.	.	.	.	.		
Phlomis tuberosa	+	r	.	.	.	r	r	.	r	.	r	.	.	.	r	r	r	.	r	r	.	1	.	r	r	.	.	r	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	
Polygonatum odoratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
D.S. All. Calamagrostio epigei-Betulion pendulae																																													
Filipendula ulmaria	1	r	+	1	2	r	r	r	r	r	r	1	1	1	r	.	r	1	r	+	r	r	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Lysimachia vulgaris	+	r	r	r	r	+	+	r	r	r	r	r	+	r	r	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
D.S. Ass. Phalaroido-Betuletum pendulae																																													
Calamagrostis canescens	1	.	2	3	r	r	4	4	r	2	+	+	2	2	2	.	.	.	.	.	r	3	.	1	.	2	2	r	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Sample nr. 10 36 27 55 3 17 33 26 31 35 22 12 8 56 23 11 34 61 48 14 21 45 39

D.S. Cl. Brachypodio pinnati-Betuletea pendulae

Rubus saxatilis	3	2	r	.	2	2	3	2	3	.	2	+	r	.	r	.	.	.	.	.
Pulmonaria mollis	r	.	1	+	r	r	.	r	r	.	.	.	.	.	.	r	.	r	.	.
Angelica sylvestris	r	.	.	+	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
Vicia sepium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	r	.
Calamagrostis arundinacea	3	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Brachypodium pinnatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Serratula coronata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium umbellatum	.	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Pleurospermum uralense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

D.D. Ord. Calamagrostio epigei-Betuletalia pendulae

Kadenia dubia	.	r	r	r	r	r	.	r	r	.	r	.	.	r	.	1	r	2	r	.	r	.	r	.
Heracleum sibiricum	+	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis epigejos	2	.	.	.	2	2	.	.	.	.	.	.	.	3	.	2	.	.	.	.	.	.	.	.

tum pendulae = D.S. All. Peucedano morisonii-Betulion pendulae

Fragaria viridis	r	.	+	.	r	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Filipendula vulgaris	.	r	.	r	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Phlomis tuberosa	r	.	.	.	r	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Polygonatum odoratum	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.

D.S. All. Calamagrostio epigei-Betulion pendulae

Filipendula ulmaria	r	.	.	2	r	+	.	.	r	.	3	r	.	.	.	r	.	r	.	.	.	.	.	.
Lysimachia vulgaris	.	r	.	r	.	r	+	.	.	r	2	+	.	.	.	r	r	r	2	1	+	.	.	.

D.S. Ass. Phalaroido-Betuletum pendulae

Calamagrostis canescens	.	.	.	.	2	4	+	r	3	2	5	3	.	4	3	.	3	3	5	4	r	.	.	.
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c) Complete list of all species found in the assessed plots.

Nomenclature follows Cherepanov (1995). hl = herb layer; s = shrub layer; t1 & t2 = tree layer 1 & 2

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Achillea millefolium</i>	hl	37	67	
<i>Adenophora lilifolia</i>	hl	2	.	
<i>Aegopodium podagraria</i>	hl	6	2	
<i>Agrimonia pilosa</i>	hl	37	.	
<i>Agrimonia procera</i>	hl	3	.	
<i>Agrostis gigantea</i>	hl	3	.	
<i>Agrostis stolonifera</i>	hl	19	17	
<i>Agrostis tenuis</i>	hl	3	33	
<i>Alchemilla xanthochlora</i>	hl	2	.	
<i>Allium angulosum</i>	hl	.	9	
<i>Allium species</i>	hl	.	2	
<i>Alopecurus pratensis</i>	hl	2	23	
<i>Amoria hybrida</i>	hl	.	2	<i>Trifolium hybridum</i>
<i>Amoria repens</i>	hl	3	11	<i>Trifolium repens</i>
<i>Androsace septentrionalis</i>	hl	.	8	
<i>Anemone sylvestris</i>	hl	14	2	
<i>Angelica palustris</i>	hl	.	2	
<i>Angelica sylvestris</i>	hl	44	.	
<i>Antennaria dioica</i>	hl	.	2	
<i>Arabidopsis thaliana</i>	hl	.	.	
<i>Arabis sagittata</i>	hl	.	2	
<i>Arctium tomentosum</i>	hl	2	2	
<i>Artemisia marshalliana</i>	hl	2	32	
<i>Artemisia laciniata</i>	hl	17	12	
<i>Artemisia pontica</i>	hl	13	26	
<i>Artemisia species</i>	hl	.	5	
<i>Artemisia vulgaris</i>	hl	13	5	
<i>Asparagus officinalis</i>	hl	6	6	
<i>Aster species</i>	hl	.	17	
<i>Astragalus danicus</i>	hl	.	38	
<i>Avenella flexuosa</i>	hl	3	.	<i>Deschampsia flexuosa</i>
<i>Barbarea stricta</i>	hl	3	.	
<i>Berteroa incana</i>	hl	.	3	
<i>Betula pendula</i>	t1	95	.	
<i>Betula pendula</i>	t2	30	.	
<i>Betula pendula</i>	s	33	.	
<i>Betula pendula</i>	hl	41	5	
<i>Bolboschoenus maritimus</i>	hl	.	2	
<i>Brachypodium pinnatum</i>	hl	27	.	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Bromopsis inermis</i>	hl	8	30	<i>Bromus inermis</i>
<i>Cacalia hastata</i>	hl	2	.	
<i>Calamagrostis arundinacea</i>	hl	38	.	
<i>Calamagrostis canescens</i>	hl	59	.	
<i>Calamagrostis epigeios</i>	hl	25	30	
<i>Calla palustris</i>	hl	2	.	
<i>Caltha palustris</i>	hl	3	.	
<i>Campanula cervicaria</i>	hl	3	.	
<i>Campanula glomerata</i>	hl	8	.	
<i>Campanula patula</i>	hl	.	12	
<i>Campanula sibirica</i>	hl	.	3	
<i>Carex acutiformis</i>	hl	24	6	
<i>Carex distans</i>	hl	.	3	
<i>Carex disticha</i>	hl	8	15	
<i>Carex hartmanii</i>	hl	6	2	
<i>Carex praecox</i>	hl	8	48	
<i>Carex species</i>	hl	8	3	
<i>Carex supina</i>	hl	.	17	
<i>Carex tomentosa</i>	hl	.	24	
<i>Carum carvi</i>	hl	.	12	
<i>Centaurea jacea</i>	hl	.	2	
<i>Centaurea scabiosa</i>	hl	2	15	
<i>Centaurea species</i>	hl	.	8	
<i>Cerastium species</i>	hl	.	2	
<i>Cerasus fruticosa</i>	s	2	.	<i>Prunus fruticosa</i>
<i>Cerasus fruticosa</i>	hl	2	.	<i>Prunus fruticosa</i>
<i>Chamaenerion angustifolium</i>	hl	13	.	<i>Epilobium angustifolium</i>
<i>Chimaphila umbellata</i>	hl	3	.	
<i>Cichorium intybus</i>	hl	.	3	
<i>Cirsium arvense</i>	hl	49	32	
<i>Cirsium esculentum</i>	hl	.	8	
<i>Cirsium species</i>	hl	.	5	
<i>Comarum palustre</i>	hl	2	2	
<i>Convolvulus arvensis</i>	hl	.	9	
<i>Crepis sibirica</i>	hl	11	.	
<i>Cypripedium calceolus</i>	hl	2	.	
<i>Dactylis glomerata</i>	hl	3	.	
<i>Deschampsia cespitosa</i>	hl	5	6	
<i>Dianthus species</i>	hl	.	2	
<i>Dracocephalum ruyschiana</i>	hl	11	12	
<i>Dryopteris carthusiana</i>	hl	13	.	
<i>Eleocharis uniglumis</i>	hl	.	2	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Elytrigia repens</i>	hl	49	55	<i>Elymus repens</i>
<i>Epilobium montanum</i>	hl	5		
<i>Epilobium tetragonum</i>	hl	.	2	
<i>Epipactis helleborine</i>	hl	6	.	
<i>Equisetum arvense</i>	hl	2	3	
<i>Equisetum fluviatile</i>	hl	2	.	
<i>Equisetum hyemale</i>	hl	10	.	
<i>Equisetum palustre</i>	hl	2	2	
<i>Equisetum pratense</i>	hl	37	.	
<i>Equisetum sylvaticum</i>	hl	2	.	
<i>Eremogone saxatilis</i>	hl	.	5	<i>Arenaria procera</i>
<i>Erigeron acris</i>	hl	.	8	
<i>Eryngium planum</i>	hl	.	6	
<i>Euphorbia esula</i>	hl	.	3	
<i>Euphrasia stricta</i>	hl	.	2	
<i>Festuca pratensis</i>	hl	2	9	
<i>Festuca pseudovina</i>	hl	.	6	<i>Festuca valesiaca subsp. parviflora</i>
<i>Festuca rubra</i>	hl	2	.	
<i>Festuca rupicola</i>	hl	8	62	
<i>Filipendula ulmaria</i>	hl	59	48	
<i>Filipendula vulgaris</i>	hl	35	39	
<i>Fragaria vesca</i>	hl	10	.	
<i>Fragaria viridis</i>	hl	37	45	
<i>Frangula alnus</i>	s	8	.	
<i>Frangula alnus</i>	hl	6	.	
<i>Galatella biflora</i>	hl	8	24	
<i>Galeopsis tetrahit</i>	hl	2	.	
<i>Galium aparine</i>	hl	13	.	
<i>Galium boreale</i>	hl	78	47	
<i>Galium palustre</i>	hl	.	2	
<i>Galium uliginosum</i>	hl	.	5	
<i>Galium verum</i>	hl	16	67	
<i>Gentiana pneumonanthe</i>	hl	5	2	
<i>Geranium pseudosibiricum</i>				
<i>et pratense</i>	hl	49	15	
<i>Geranium sylvaticum</i>	hl	8	.	
<i>Geum urbanum</i>	hl	6	3	
<i>Glaux maritima</i>	hl	.	3	
<i>Glechoma hederacea</i>	hl	8	23	
<i>Helictotrichon desertorum</i>	hl	.	9	
<i>Heracleum sphondylium</i>	hl	34	6	
<i>Hieracium species</i>	hl	.	3	
<i>Hieracium umbellatum</i>	hl	27	3	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Hierochloe odorata</i>	hl	8	12	
<i>Hordeum brevisubulatum</i>	hl	.	14	
<i>Hylotelephium maximum</i>	hl	15	2	<i>Sedum maximum</i>
<i>Hypericum perforatum</i>	hl	3	.	
<i>Hypochoeris radicata</i>	hl	.	2	
<i>Inula britannica</i>	hl	.	8	
<i>Inula hirta</i>	hl	.	2	
<i>Inula salicina</i>	hl	52	11	
<i>Iris sibirica</i>	hl	11	9	
<i>Juncus compressus</i>	hl	.	12	
<i>Juncus species</i>	hl	.	2	
<i>Kadenia dubia</i>	hl	73	45	<i>Cnidium dubium</i>
<i>Knautia arvensis</i>	hl	6	.	
<i>Koeleria macrantha</i>	hl	.	8	
<i>Lactuca sibirica</i>	hl	14	.	
<i>Lathyrus palustris</i>	hl	6	2	
<i>Lathyrus pisiformis</i>	hl	27	3	
<i>Lathyrus pratensis</i>	hl	43	47	
<i>Lathyrus species</i>	hl	.	2	
<i>Lathyrus tuberosus</i>	hl	2	9	
<i>Lathyrus vernus</i>	hl	13	5	
<i>Leucanthemum vulgare</i>	hl	.	5	
<i>Leymus arenarius</i>	hl	.	12	
<i>Lilium martagon</i>	hl	13	.	
<i>Limonium gmelinii</i>	hl	.	20	
<i>Linaria vulgaris</i>	hl	.	20	
<i>Lithospermum officinale</i>	hl	5	11	
<i>Lupinaster pentaphyllus</i>	hl	29	17	
<i>Luzula multiflora</i>	hl	2	9	
<i>Lycopodium clavatum</i>	hl	3	.	
<i>Lycopus europaeus</i>	hl	13	2	
<i>Lysimachia vulgaris</i>	hl	60	11	
<i>Lythrum salicaria</i>	hl	17	3	
<i>Maianthemum bifolium</i>	hl	17	.	
<i>Medicago falcata</i>	hl	.	12	
<i>Melampyrum cristatum</i>	hl	5	24	
<i>Melampyrum pratense</i>	hl	3	.	
<i>Melandrium album</i>	hl	2	8	<i>Silene alba</i>
<i>Melilotus officinalis</i>	hl	.	2	
<i>Menyanthes trifoliata</i>	hl	2	.	
<i>Milium effusum</i>	hl	5	.	
<i>Moehringia lateriflora</i>	hl	24	.	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Molinia caerulea</i>	hl	5	.	
<i>Myosotis ramosissima</i>	hl	.	21	
<i>Naumburgia thyrsiflora</i>	hl	5	.	<i>Lysimachia thyrsiflora</i>
<i>Nonea pulla</i>	hl	.	2	
<i>Odontites vulgaris</i>	hl	.	2	
<i>Origanum vulgare</i>	hl	16	5	
<i>Orobanche alsatica</i>	hl	.	2	
<i>Orobanche species</i>	hl	8	.	
<i>Orthilia secunda</i>	hl	25	.	
<i>Padus avium</i>	t2	3	.	<i>Prunus padus</i>
<i>Padus avium</i>	s	2	.	<i>Prunus padus</i>
<i>Padus avium</i>	hl	5	.	<i>Prunus padus</i>
<i>Paris quadrifolia</i>	hl	6	.	
<i>Pedicularis species</i>	hl	.	5	
<i>Persicaria amphibia</i>	hl	.	3	
<i>Peucedanum morisonii</i>	hl	5	26	
<i>Peucedanum species</i>	hl	.	2	
<i>Phalacrolooma annuum</i>	hl	.	2	<i>Erigeron annuus</i>
<i>Phalaroides arundinacea</i>	hl	8	2	<i>Phalaris arundinacea</i>
<i>Phleum phleoides</i>	hl	2	42	
<i>Phleum pratense</i>	hl	5	.	
<i>Phlomis tuberosa</i>	hl	35	32	<i>Phlomis tuberosa</i>
<i>Phragmites australis</i>	hl	22	.	
<i>Pimpinella saxifraga</i>	hl	48	32	
<i>Pinus sylvestris</i>	t1	3	.	
<i>Pinus sylvestris</i>	t2	2	.	
<i>Pinus sylvestris</i>	s	3	.	
<i>Pinus sylvestris</i>	hl	3	.	
<i>Plantago intermedia</i>	hl	.	3	
<i>Plantago lanceolata</i>	hl	.	3	
<i>Plantago major</i>	hl	5	5	
<i>Plantago maritima</i>	hl	.	9	
<i>Plantago maxima</i>	hl	5	26	
<i>Plantago media</i>	hl	3	36	
<i>Plantago urvillei</i>	hl	.	11	<i>Plantago stepposa</i>
<i>Platanthera bifolia</i>	hl	6	.	
<i>Pleurospermum uralense</i>	hl	14	.	
<i>Poa annua</i>	hl	2	.	
<i>Poa compressa</i>	hl	.	3	
<i>Poa nemoralis</i>	hl	13	.	
<i>Poa palustris</i>	hl	.	2	
<i>Poa pratensis</i>	hl	21	91	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Poa trivialis</i>	hl	5	3	
<i>Polemonium caucasicum</i>	hl	2	.	
<i>Polygala sibirica</i>	hl	.	8	
<i>Polygonatum odoratum</i>	hl	25	.	
<i>Polygonum aviculare</i>	hl	.	2	
<i>Populus tremula</i>	t1	17	.	
<i>Populus tremula</i>	t2	6	.	
<i>Populus tremula</i>	s	24	.	
<i>Populus tremula</i>	hl	40	.	
<i>Potentilla anserina</i>	hl	5	35	
<i>Potentilla argentea</i>	hl	3	67	
<i>Potentilla bifurca</i>	hl	.	3	
<i>Potentilla chrysantha</i>	hl	.	3	
<i>Potentilla erecta</i>	hl	14	.	
<i>Potentilla heptaphylla</i>	hl	.	5	
<i>Potentilla recta</i>	hl	.	2	
<i>Potentilla reptans</i>	hl	2	.	
<i>Potentilla species</i>	hl	.	6	
<i>Prunella vulgaris</i>	hl	6	2	
<i>Ptarmica salicifolia</i>	hl	10	15	<i>Achillea salicifolia</i>
<i>Pteridium aquilinum</i>	hl	2	.	
<i>Pulmonaria mollis</i>	hl	71	6	
<i>Pulsatilla patens</i>	hl	10	.	
<i>Pyrola rotundifolia</i>	hl	11	.	
<i>Ranunculus acris</i>	hl	8	45	
<i>Ranunculus auricomus</i>	hl	2	.	
<i>Ranunculus lingua</i>	hl	6	.	
<i>Ranunculus repens</i>	hl	5	12	
<i>Rhinanthus serotinus</i>	hl	.	5	<i>Rhinanthus angustifolius</i>
<i>Ribes nigrum</i>	hl	19	.	
<i>Rorippa species</i>	hl	2	2	
<i>Rosa majalis</i>	s	14	.	
<i>Rosa majalis</i>	hl	56	17	
<i>Rubus saxatilis</i>	hl	79	3	
<i>Rumex acetosa</i>	hl	11	15	
<i>Rumex acetosella</i>	hl	.	3	
<i>Rumex confertus</i>	hl	.	8	
<i>Rumex crispus</i>	hl	.	9	
<i>Rumex species</i>	hl	.	2	
<i>Salix aurita</i>	s	16	.	
<i>Salix aurita</i>	hl	10	.	
<i>Salix species</i>	hl	.	5	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Sanguisorba officinalis</i>	hl	37	29	
<i>Saussurea salsa</i>	hl	.	2	
<i>Scorzonera parviflora</i>	hl	.	6	
<i>Scutellaria galericulata</i>	hl	2	2	
<i>Scutellaria hastifolia</i>	hl	.	2	
<i>Senecio jacobaea</i>	hl	.	6	
<i>Senecio species</i>	hl	.	2	
<i>Serratula coronata</i>	hl	30	12	
<i>Seseli libanotis</i>	hl	5	29	
<i>Silene nutans</i>	hl	10	20	
<i>Solanum dulcamara</i>	hl	8	.	
<i>Solidago virgaurea</i>	hl	25	.	
<i>Sonchus arvensis</i>	hl	3	9	
<i>Sorbus aucuparia</i>	s	6	.	
<i>Sorbus aucuparia</i>	hl	3	.	
<i>Sorbus species</i>	s	2	.	
<i>Stachys palustris</i>	hl	27	3	
<i>Stachys sylvatica</i>	hl	2	.	
<i>Stellaria graminea</i>	hl	.	45	
<i>Stellaria holostea</i>	hl	2	.	
<i>Stellaria palustris</i>	hl	.	3	
<i>Stellaria species</i>	hl	.	2	
<i>Stipa zalesskii</i>	hl	.	12	
<i>Succisa pratensis</i>	hl	3	.	
<i>Tanacetum vulgare</i>	hl	2	5	
<i>Taraxacum officinale</i>	hl	16	64	
<i>Thalictrum species</i>	hl	38	49	
<i>Thesium arvense</i>	hl	.	3	
<i>Tilia cordata</i>	t1	2	.	
<i>Tilia cordata</i>	t2	2	.	
<i>Tilia cordata</i>	s	2	.	
<i>Tilia cordata</i>	hl	6	.	
<i>Tragopogon orientalis</i>	hl	.	5	<i>Tragopogon pratensis ssp. orientalis</i>
<i>Trifolium medium</i>	hl	19	.	
<i>Trifolium pratense</i>	hl	10	27	
<i>Triglochin palustre</i>	hl	.	2	
<i>Tripleurospermum maritimum</i>	hl	.	6	
<i>Tripolium pannonicum</i>	hl	.	3	<i>Aster tripolium</i>
<i>Trollius europaeus</i>	hl	3	.	
<i>Trommsdorfia maculata</i>	hl	.	15	
<i>Urtica dioica</i>	hl	14	.	
<i>Vaccinium myrtillus</i>	hl	3	.	

Ecosystem		Forest	Grassland	
N		63	66	Synonyms
	Layer	Frequency		Wißkirchen & Haeupler 1998
<i>Vaccinium vitis-idaea</i>	hl	6	.	
<i>Valeriana officinalis</i>	hl	.	2	
<i>Veronica chamaedrys</i>	hl	3	.	
<i>Veronica longifolia</i>	hl	33	8	
<i>Veronica prostrata</i>	hl	.	2	
<i>Veronica species</i>	hl	.	3	
<i>Veronica spicata</i>	hl	.	50	
<i>Veronica spuria</i>	hl	.	15	<i>Pseudolysimachion spurium</i>
<i>Veronica teucrium</i>	hl	11	.	
<i>Viburnum opulus</i>	hl	8	.	
<i>Vicia cracca</i>	hl	48	59	
<i>Vicia pisiformis</i>	hl	2	.	
<i>Vicia sepium</i>	hl	57	21	
<i>Vicia tenuifolia</i>	hl	3	15	
<i>Viola collina</i>	hl	25	.	
<i>Viola persicifolia</i>	hl	2	12	
<i>Viola rupestris</i>	hl	.	5	
<i>Viola species</i>	hl	.	2	
<i>XFestulolium loliaceum</i>	hl	3	.	
<i>species richness</i>		186	201	
<i>species richness total</i>		289		

Eigenständigkeitserklärung

Ich versichere, dass ich diese Arbeit einschließlich der beigelegten Abbildungen, Tabellen, Karten und Fotos, soweit nicht anders gekennzeichnet, selbst angefertigt und keine als die angegebenen Hilfsmittel benutzt habe. Alle Textstellen, die im Wortlaut oder Sinn aus anderen Werken entstammen, sind unter Angabe der Quelle gekennzeichnet.

Münster, den 16.Juli 2013

Kathrin Gottbehüt

