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Floristic composition and environmental determinants of pine forests in the hemiboreal zone of Western Siberia

Floristische Zusammensetzung und bestimmende Umweltfaktoren in Kiefernwäldern in der hemiborealen Zone West-Sibiriens

Martin Freitag[1,] *, Wanja Mathar[1], Andrei A. Yurtaev[2] & Norbert Hölzel[1]

[1]*Biodiversity and Ecosystem Research Group, Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany, martin.freitag@uni-muenster.de; w.mathar@uni-muenster.de; norbert.hoelzel@uni-muenster.de;*
[2]*Tyumen State University, Semakova Str. 10, Tyumen 625023, Russia, yurtaevgeo@yandex.ru*
**Corresponding author*

Abstract

Despite their vast distribution ranging from Central Europe to Siberia, hemiboreal oligotrophic pine forests remain poorly studied. Though they dependence on low productive soils, they are widespread on sandy deposits or in bogs. This study aims to classify and ecologically describe the vegetation of oligotrophic pine forests in the south of Western Siberia.

In total 50 relevés from nutrient-poor sandy substrates and bogs were sampled in the pre-Taiga zone of the Tyumen province covering the whole range from dry to wet habitats. Five vegetation types were defined by hierarchical clustering. Phi coefficient of association was calculated for groups and their combination, resulting in a high number of species with high fidelity to clusters. Floristic composition ranged from xero-mesophytic vegetation with high frequency of the tribe *Pyroleae* on dry sandy soils to pine-sphagnum-communities on bogs. The strongest environmental gradients influencing the floristic composition were soil humidity, nutrient supply and fire. Higher nutrient supply due to loamy subsoil increased vascular plant species richness, enabling common plants of hemiboreal birch forests to grow.

Surface fires turned out to be a key process in dry pine forests, resulting in a destroyed bryophyte layer and to a partly altered vascular plant species composition. Fire regime plays an important role in maintaining the floristic composition and habitat structure over time. West-Siberian dry oligotrophic pine forests are ecologically, structurally and floristically quite similar to Central-European pine communities of the *Peucedano-Pinetum*.

Keywords: classification, hemiboreal forest, *Peucedano-Pinetum*, *Pinus sylvestris*, *Pyroleae*; Tyumen, wild fire

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

In Western Siberia, hemiboreal forests occur in a narrow transition zone between the true boreal (taiga) and the forest steppe zone (ERMAKOV et al. 2000). They are built up by few light-demanding deciduous (*Betula pendula, B. pubescens*, *Populus tremula*) and coniferous trees (*Pinus sylvestris*) forming a relatively open canopy. Analogous to open habitats, in

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these forests there is a remarkable overlap in the plant species pool between Western Siberia and Europe (ERMAKOV 2010). This biogeographic pattern is also reflected by the term 'Euro-Siberian Vegetation circle' that is commonly used in European phytosociology to emphasise the high similarity in the floristic composition of related temperate plant communities in Europe and Western Siberia. Due to the remoteness of forests in Siberia and the lack of studies focussing on species composition, little is known about the habitat-level relationship between site and vegetation (SPRIBILLE & CHYTRÝ 2002). Within the last decade, several studies provided data about diversity patterns and site characteristics of hemiboreal forests in the southern Ural mountains (CHYTRÝ et al. 2010) and in the Altai and Sayan mountains in Southern Siberia (CHYTRÝ et al. 2008, CHYTRÝ et al. 2012). This recent research focused on hemiboreal forest communities of meso- to eutrophic, fertile loamy soils. Similarly, an eminent phytosociological study, applying the Braun-Blanquet-approach to hemiboreal forests from the Southern Urals in the West to northern Mongolia in the East by ERMAKOV et al. (2000) largely focused on mesic forest communities and neglected Pine-dominated oligotrophic communities. Comparable studies of oligotrophic pine forests on sandy substrates have been studied in Southern Central Siberia (POLYAKOVA & ERMAKOV 2008; POLYAKOVA et al. 2008), whilst studies considering West Siberian pine forests at regional (ERMAKOV & MAKHATKOV 2011, PEREVOZNIKOVA et al. 2007) and Eurasian scale (ERMAKOV & MO-ROZOVA 2011) focused exclusively on boreal pine forests. Overall, studies on pine forests in the hemiboreal and forest steppe zone Western Siberia are scarce.

In the South of the Western Siberian Plain, *Pinus sylvestris* forests occur on extensive sandy glacio-fluvial and aeolian deposits, which are typically found along the terraces of large lowland rivers. Their ground vegetation consists of bryophytes, lichens and xero-mesophytic herbs, representing a widespread, ecologically and floristically distinctive western Eurasian pine-forest type (ERMAKOV & MOROZOVA 2011, PEREVOZNIKOVA et al. 2007). The warm, dry sites are characterised by xero-mesophytic species such as *Antennaria dioica*, *Chimaphila umbellata* and *Pyrola chlorantha* (ERMAKOV et al. 2000, ERMAKOV & MAKHATKOV 2011). On moister sites, the abundance of *Vaccinium myrtillus* and *V. vitis-idaea* increases, whereas the occurrence of *Ledum palustre* and decreasing number of xero-mesophytes indicate wet, cold soils (ERMAKOV & MOROZOVA 2011). The bryophyte layer is dominated by the widespread species *Pleurozium schreberi* and *Hylocomium splendens* (PEREVOZNIKOVA et al. 2007, SPRIBILLE & CHYTRÝ 2002). The species inventory is surprisingly similar to the *Dicrano-Pinion* (Libbert 1933) W. Matuszkiewicz 1962, which occurs in Central and Eastern Europe. The eastern border of the distribution *Dicrano-Pinion* communities is still unclear, but HEINKEN (2008b) suspects the range to reach the river terraces of Ob and Tom in the south of Western Siberia. Under the rather dry and warm climatic conditions in southern Western Siberia, communities rich in *Pyroloideae* (e.g. *Chimaphila umbellata*, *Pyrola chlorantha*) and basiphilous, xero-mesophytic herbs (e.g. *Pulsatilla patens* ssp. *flavescens*, *Carex ericetorum*, *Viola rupestris*, *Antennaria dioica*, *Polygonatum odoratum*) are the predominant type of pine forest on dry sandy deposits. These West-Siberian pine forests are presumed to show a high floristic similarity to analogous communities described from Poland and Germany such as the *Peucedano-Pinetum* W. Matuszkiewicz 1962 (HEINKEN 2008b). In Central and Eastern Europe these *Pyroloideae*-rich communities have become very rare since the middle of the last century and in Germany they are currently at the brink of extinction (RENNWALD 2000). From Poland, a decline has been reported as well (HEINKEN 2008b), but a recent study showed that several of the characteristic species were able to establish in pine plantations on former arable fields (MATUSZKIEWICZ et al. 2013).

The reason for this tremendous decline are not fully understood but eutrophication and acidification processes due to high atmospheric nitrogen depositions and the abandonment of traditional management such as litter raking (PRIETZEL & KAISER 2005) seem to play a prominent role for the serious decline of many characteristic species (HEINKEN 2008a). Stands of the *Peucedano-Pinetum* in Central and Eastern Europe appear to be almost completely dependent on adequate disturbance regime that halt or interrupt succession and soil acidification. However, there is great uncertainty about the kind and intensity of management intervention mimicking natural disturbances. This situation is worsened by the fact, that there are almost no reference stands of adequate size left. Thus, it could be extremely useful having a closer look to disturbance regimes and site conditions within the core areas of distribution such as southern Western Siberia.

In these continental regions fire is a major ecological factor shaping the structure and floristic composition of pine forests (CONARD & IVANOVA 1997, WIRTH 2005). Once a natural disturbance factor, today's fire events are often caused by human activities (e.g. camp fires, CONARD & IVANOVA 1997, JUPP et al. 2006). Recurring fires preserve an open canopy structure and promote the dominance of pine, as *Pinus sylvestris* is able to resist light surface fires (WIRTH 2005; ADÁMEK et al. 2015). Surface fires especially enable light-demanding low-competitive species to grow in the forest (NUZZO et al. 1996) and may enhance species richness (MAROZAS et al. 2007). However, most of these findings come from more mesic boreal pine forests and it remains questionable how they translate to more xero-mesic *Pyroloideae*-rich communities of the hemiboreal zone.

To close this gap of knowledge we studied pine forests in the transition between boreal zone and forest-steppe in the South of Western Siberia around the city of Tyumen. In this region extensive pine stands occur, offering excellent conditions to study structure, floristic composition and dynamics of continental temperate pine forests along fire recurrence, substrate and topographic moisture gradients. From our analysis, we expect valuable insights for the conservation and management of *Pyroloideae*-rich pine forests in Central and Eastern Europe. Specifically we asked the following questions: (1) Which main ecological gradients determine the floristic composition of Western Siberian oligotrophic pine forest? (2) How does fire affect stand structure and the composition of the ground vegetation? (3) Are pine forests of the West Siberian forest steppe zone related to *Pyroloideae*-rich oligotrophic pine forests in Central Europe?

2. Study area

The West Siberian Plain is an extensive lowland area east of the Ural mountains, bordered to the south by the Kazakh highlands, to the east by the Irtysh Basin and to the north by the Ob lowlands (ZAKH et al. 2010). The study area is located in the southern part of the West Siberian plain in the Oblast Tyumen, around the city of Tyumen (57°9′N/65°32′O, Fig. 1), Russian Federation. It is part of the hemiboreal (boreonemoral) zone, situated in a narrow transition zone between the southern taiga to the north and the forest steppe to the south (OLSON et al. 2001). Elevation varies between 50 and 150 m a.s.l. The study area is drained by the Tura River in the northern part and the Tobol River in the southern part. Especially to the north of the city of Tyumen, peatlands cover a large proportion of the surface (around 40%, SHENG et al. 2004). *Pinus sylvestris* forests on peatlands occur as pine-sphagnum communities in depressions on a shallow peat layer as well as in bogs with peat depth of several meters.

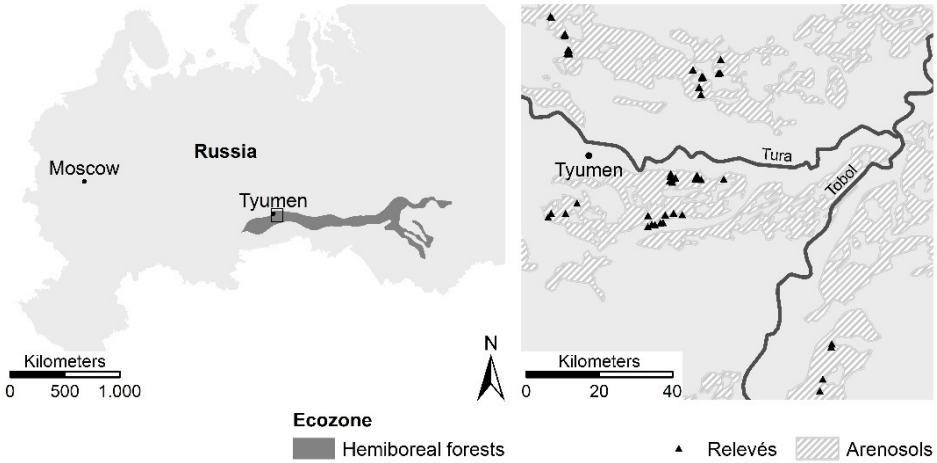

Fig. 1. Location of the relevés in the study area in the Oblast Tyumen, Russia (Basemap: GLOBAL ADMINISTRATIVE AREAS 2012; Ecozones: OLSON et al. 2001).

Abb. 1. Lage der Aufnahmen im Untersuchungs-Gebiet im Oblast Tyumen, Russland (Hintergrundkarte: GLOBAL ADMINISTRATIVE AREAS 2012; Ökozonen: OLSON et al. 2001).

The substrate consists of sandy and loamy deposits in varying proportions, formed by aeolian and alluvial processes during the Quarternary (SELEZNEVA 1973). The vast floodplains are prevailed by Gleysols and wet organic soils, mostly used as meadows and hayfields (SELEZNEVA 1973). Degraded chernozems and grey forest soils occur in the well-drained areas. If not used for agriculture, these soils are dominated by birch forests (*Betula pendula*) with varying cover of the subdominant *Populus tremula*. Slightly podzolic, sandy soils (Podzolic Regosols) as found on old dunes and higher river terraces are dominated by *Pinus sylvestris* (BLYAKHARCHUK 2003, NIMIS et al. 1994, SELEZNEVA 1973). Frequent fires influence forests in the study area.

The climate is slightly humid and highly continental with warm summers (mean July temperature +17.8 °C) and cold and relatively dry winters (mean January temperature -17 °C). Mean annual precipitation is 476 mm, of which two thirds fall between May and September (RUSSIAN FEDERAL SERVICE FOR HYDROMETEOROLOGY AND ENVIRONMENTAL MONITORING).

3. Methods

3.1 Data sampling

The study area around the city of Tyumen was chosen according to the main distribution of sandy substrates in the region of Tyumen, which predominantly occur at the river terraces of the large rivers Tura and Tobol (Fig. 1). Within this area, we analysed all types of Pine (*Pinus sylvestris*) -dominated forest ranging from dry sandy soils with prevailing xero-meosphytic ground vegetation to the opposite end of the moisture gradient with a *Sphagnum* dominated understory on peat soils. In June and July 2014, we sampled 50 relevés of 10 x 10 m². In each relevé, we recorded all vascular plants, ground-dwelling bryophytes and macro-lichens and estimated their cover using a modified Braun-Blanquet scale (VAN DER MAAREL 1979). Bryophytes of the genus *Sphagnum* and lichens of the genus *Cladonia*

were merged at the genus level in all statistical analysis as not all specimens could be identified to species level in each relevé. In addition to individual species cover, we estimated total cover of all structural layers (tree, shrub, herb, bryophyte, lichen, litter) and average height of the herb layer. Average heights of shrub- and tree-layers were measured with an inclinometer. Species and environmental data were stored in a TurboVeg database (HENNEKENS & SCHAMINÉE 2001) and are available in the Supplement E1. Nomenclature of vascular plants follows CZEREPANOV (1995), except for *Kadenia dubia*, which was treated as *Cnidium dubium* (Schkuhr) Thell. Bryophytes follow IGNATOV et al. (2006), lichens follow ESSLINGER (2014). A list of synonyms covered by WISSKIRCHEN & HAEUPLER (1998) can be found in the Supplement E2.

In addition to floristic data, the following variables were measured:

Mixed soil samples were taken from five pooled cores in the plot at a depth level of 0–5 cm and 5–30 cm. Soil pH was measured from depth level 5–30 cm on mineral soil and from 0–5 cm on peat soils (peat depth > 30cm). Soil was shaken in distilled water (mass ratio 1:2.5) for 20 minutes and then measured after two hours. Soil depth and thickness of the litter layer were determined at one soil core within the plot.

The impact of burning was estimated considering the amount and height of scorch marks at trees within the plot and evaluated on ordinal scale with three levels. Sites with frequent trees having scorch marks higher than 1.5 meters were considered as strongly burnt and sites with trees having scorch marks between 1.5 and 0.5 m as medium-burnt. Sites were trees had only sporadically scorch marks or only low scorch marks were considered as weakly burnt. Although most pine forests showed signs of fire, we seldom found pine trees with deep fire scars indicating that fire mostly affects the understory vegetation.

Using the ecological scales of DIDUKH (2011), unweighted community means of indicator values were calculated taking in account vascular plants of the field layer (data available for 93% of the species). The percentage of leaf anatomy types scleromorph (as an adaption to drought and nutrient depletion) and mesomorph (without adaptions to drought or wetness) of vascular plant species of the field layer was calculated using fuzzy coded values (KLOTZ et al. 2002, data available for 92% of the species).

3.2 Data analysis

3.2.1 Data preparation

Prior the analysis, species cover codes were transformed to mean percentage values (VAN DER MAAREL 1979) and square-root transformed to downsize the effect of large cover values. Species occurring in less than three relevés were removed to minimise the noise in the dataset.

3.2.2 Classification

Community types were defined according to their species composition using the hierarchical clustering method flexible beta ($\beta = -0.25$) with Bray-Curtis distance. The resulting dendrogram was cut into five groups at 45% dissimilarity.

Species' fidelity to each cluster was defined by Pearson's *phi coefficient of association* (Φ) corrected for unequal group sizes (TICHÝ & CHYTRÝ 2006) and tested for significance with a Monte-Carlo-permutation-test (1000 permutations, significant $p < 0.05$). Species with significant Φ-values of at least 0.2 were considered as characteristic. If a species had significant Φ-values ≥ 0.2 for more than one group, a Φ- and the corresponding p-value were calculated for the group combination (DE CÁCERES et al. 2010).

Clusters were named after one 'character species' in combination with the dominant tree species *Pinus sylvestris*. They were classified into phytosociological classes according to HEINKEN (2008b) in case of class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 and WAGNER & WAGNER (2007) in case of class *Vaccinio uliginosae Pinetea* Passarge et G. Hofmann 1968.

To test for significant differences of environmental variables between clusters, we performed ANOVA and Tukey's test in case of normal distribution and homoscedasticity (which was assumed if both Kolmogorov-Smirnov- and Levene-test revealed a *p*-value ≥ 0.05), otherwise non-parametric Kruskal-Wallis-H- and pairwise Mann-Whitney-U-tests were performed. *P*-values were adjusted for multiple comparisons with Bonferroni correction.

3.2.3 Gradient analysis

Relationships between major environmental gradients, species richness and species composition were explored by Detrended Correspondence Analysis (DCA) using the 'decorana' function (R package 'vegan') with default options. Correlation between ordination axes and environmental variables were assessed using 'envfit' function. Significance of the correlation vectors was tested with 1,000 permutations.

In the following, richness is defined as the number of vascular plants in the field layer.

All statistical analyses were performed with R version 3.0.3 (R CORE TEAM 2014) including packages 'cluster' (MAECHLER et al. 2014), 'indicspecies' (DE CÁCERES & LEGENDRE 2009) and 'vegan' (OKSANEN et al. 2013).

4. Results

4.1 Classification

In total, 105 vascular plant, 10 bryophyte and 5 lichen species were recorded. The average number of species per plot including woods and cryptogams was 22 (minimum: 9, maximum: 43), the average richness in the field layer was 17 (minimum: 4, maximum: 36).

After removing rare species, 73 species were included in the cluster analysis. Cutting the tree at 45% dissimilarity resulted in five groups with sizes ranging from 7–15 relevés (Fig. 2). The first cut separated the cluster E from the tree, which coincided with high abun-

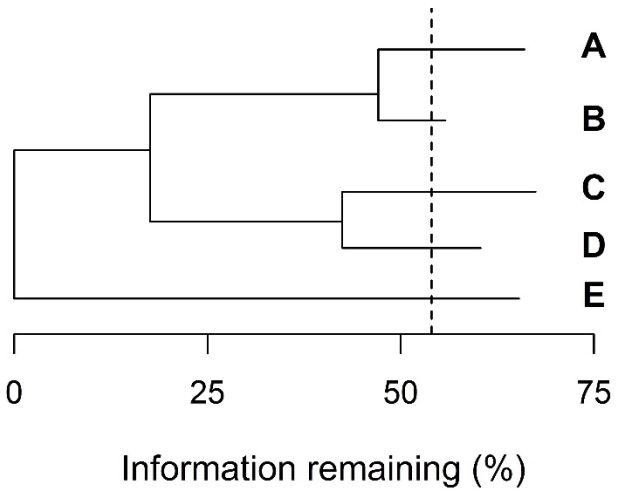

Fig. 2. Dendrogram resulting of hierarchical cluster analysis. The dashed vertical line marks the cut level at 55% information remaining. Each leaf of the dendrogram represents one cluster.

Abb. 2. Dendrogramm der hierarchischen Cluster-Analyse. Die gestrichelte vertikale Linie markiert die Schnitt-Höhe bei 55 % verbleibender Information.

dance and frequency of bog species such as *Chamaedaphne calyculata*, *Sphagnum* spp. and *Oxycoccus palustris* (Table 1). The second cut separated clusters containing xero-mesophytic species such as *Carex ericetorum*, *C. supina* and *Antennaria dioica* (cluster A and B) from those with a higher proportion of mesophilous and true forest species (cluster C and D, e.g. *Maianthemum bifolium*, *Trientalis europaea* and *Melampyrum pratense*).

Clusters were well characterized by indicative species. Overall, 46 vascular plant species and 6 bryophytes (of which one is the genus *Sphagnum*) had a significant Φ-value greater than the subjective threshold value of 0.2. Twenty-eight of them were assigned to one cluster, nineteen to the combination of two clusters (Table 1). The frequent species *Chimaphila umbellata*, *Lupinaster pentaphyllus*, *Pleurozium schreberi*, *Solidago virgaurea* and *Vaccinium vitis-idea*, occurring in more than 65% of the relevés, acted as unifying 'character species' for three clusters.

In the following the defined types are shortly described, taking into account both species inventory and environmental characteristics (Table 2). Photos of typical stands of the types can be found in Figure 4a–e.

Table 1. Field and bryophyte layer species' percentage frequency in vegetation types. Only species with significant *phi coefficient* (Φ) ≥ 0.2 are displayed. Within groups, species are ordered by decreasing Φ-value. Species with $\Phi \geq 0.6$ are shown in bold. Significance (p) was tested with a permutation test (1000 permutations) for group and group combination, respectively (p-levels: 0.05 > * > 0.01 > ** > 0.001 > ***).

Tabelle 1. Prozentuale Häufigkeit der Arten der Feld- und Moos-Schicht in den Vegetationstypen. Nur Arten mit signifikantem *phi-Koeffizient* (Φ) ≥ 0,2 sind dargestellt. Innerhalb der Gruppen sind die Arten nach abnehmendem Φ-Wert sortiert. Arten mit $\Phi \geq 0{,}6$ sind fett dargestellt. Signifikanzniveaus (p) wurden mit einem Permutationstest (1000 Permutationen) für die Gruppe beziehungsweise Gruppenkombination getestet (p-Level: 0,05 > * > 0,01 > ** > 0,001 > ***).

Cluster	**A**	**B**	**C**	**D**	**E**		
n	*9*	*15*	*9*	*10*	*7*		
No. of diagnostic species	14	17	27	10	13		
	Frequency (%)					Φ	p
Eremogone saxatilis	**56**	7	-	-	-	**0.65**	***
Polygonatum odoratum	89	47	44	-	-	0.55	***
Veronica spicata	67	40	11	-	-	0.51	**
Carex ericetorum	**100**	**87**	44	-	-	**0.77**	***
Carex supina	**67**	**47**	-	-	-	**0.66**	***
Antennaria dioica	**89**	**73**	44	10	-	**0.62**	***
Dianthus versicolor	**56**	**47**	-	-	-	**0.62**	***
Hieracium umbellatum	100	87	78	30	-	0.57	***
Pulsatilla patens subsp. *flavescens*	78	80	56	10	-	0.56	**
Pyrola chlorantha	78	60	44	20	-	0.47	**
Viola rupestris	56	53	44	-	-	0.42	*
Calamagrostis epigeios	44	87	22	40	-	0.49	**
Orthilia secunda	56	**93**	**100**	40	-	**0.64**	***
Equisetum hyemale	56	73	67	30	-	0.40	*
Cnidium dubium	11	-	**89**	-	-	**0.86**	***
Fragaria viridis	-	7	**67**	-	-	**0.73**	***

Cluster	**A**	**B**	**C**	**D**	**E**		
n	*9*	*15*	*9*	*10*	*7*		
No. of diagnostic species	14	17	27	10	13		
	Frequency (%)					*Φ*	*p*
Viola montana	-	13	**67**	10	-	**0.63**	***
Geranium pratense	-	-	**44**	-	-	**0.62**	***
Rubus saxatilis	-	47	**100**	50	-	**0.62**	***
Vicia sepium	22	27	**78**	-	-	**0.60**	***
Melica nutans	-	-	33	-	-	0.53	**
Lathyrus vernus	11	7	56	10	-	0.52	**
Pteridium aquilinum	-	7	44	10	-	0.49	**
Galium boreale	11	7	44	-	-	0.48	**
Platanthera bifolia	-	7	33	-	-	0.47	**
Pyrola rotundifolia	-	22	44	-	-	0.47	*
Achillea millefolium	11	13	44	-	-	0.44	*
Calamagrostis arundinacea	78	80	100	60	-	0.38	***
Silene nutans	22	20	44	-	-	0.36	*
Lycopodium clavatum	11	13	56	40	-	0.37	*
Maianthemum bifolium	11	27	**100**	**80**	-	**0.76**	***
Trientalis europaea	-	-	**78**	**60**	-	**0.76**	***
Melampyrum pratense	-	27	67	60	-	0.58	**
Vaccinium myrtillus	11	27	78	80	29	0.56	***
Calamagrostis canescens	-	7	33	50	-	0.50	**
Ledum palustre	-	-	22	**90**	**100**	**0.87**	***
Carex lasiocarpa	-	7	-	**70**	**86**	**0.79**	***
Chamaedaphne calyculata	-	-	-	-	**100**	**1**	***
Rubus chamaemorus	-	-	-	-	**57**	**0.72**	***
Oxycoccus palustris	-	-	-	-	**57**	**0.72**	***
Andromeda polifolia	-	-	-	-	**43**	**0.61**	**
Eriophorum vaginatum	-	-	-	-	**43**	**0.61**	**
Diagnostic species for three types							
Lupinaster pentaphyllus	**89**	**93**	**100**	30	-	**0.80**	***
Solidago virgaurea	**100**	**93**	**89**	50	-	**0.72**	***
Chimaphila umbellata	**100**	**100**	**100**	70	14	**0.67**	***
Vaccinium vitis-idaea	22	40	**89**	**100**	**100**	**0.70**	***
Bryophytes							
Hylocomium splendens	-	80	44	40	57	0.36	*
Dicranum polysetum	22	100	33	40	71	0.57	***
Pleurozium schreberi	56	100	78	100	100	0.48	**
Polytrichum commune	-	-	-	30	29	0.45	*
***Sphagnum* spp.**	-	-	-	10	**100**	**0.94**	***
Rhytidiadelphus loreus	-	-	-	-	**43**	**0.61**	***

Table 2. Synoptic table showing mean and standard deviation of structural and environmental characteristics of vegetation types. Different superscript letters indicate significant differences between groups found by Tukey-HSD (a, b, c, d) and pairwise Mann-Whitney U-Test (A, B, C, D; Bonferroni-corrected due to multiple testing). Corresponding probability-values (*p*-value) refer to ANOVA and Kruskal-Wallis-H-test, respectively (0.05 > * > 0.01 > ** > 0.001 > ***; - : not significant).

Tablle 2. Übersichtstabelle mit Mittelwerten und Standardabweichungen ausgewählter Struktur- und Umweltparameter. Hochgestellte Buchstaben stehen für signifikante Unterschiede zwischen Gruppen nach Tukey-HSD (a, b, c, d) und paarweisem Mann-Whitney U-Test (A, B, C, D; Bonferroni-korrigiert nach multiplen Tests). Die dazugehörigen Signifikanzniveaus (*p*) beziehen sich auf ANOVA und Kruskal-Wallis-H-Test (0,05 > * > 0,01 > ** > 0,001 > ***; - : nicht signifikant).

Cluster	**A**	**B**	**C**	**D**	**E**	
n	*9*	*15*	*9*	*10*	*7*	
	mean (standard deviation)					*p*
Cover (%)						
Tree layer 1	27 (6)^{a}	28 (6)^{a}	24 (4)^{a}	15 (7)^{b}	15 (9)^{b}	***
Field layer	13 (7)^{A}	15 (6)^{A}	40 (12)^{B}	39 (23)^{B}	46 (11)^{B}	***
Bryophytes	1 (1)^{a}	54 (27)$^{b, c}$	17 (21)$^{a, d}$	36 (25)$^{c, d}$	71 (21)^{b}	***
Lichens	0.8 (1.3)	0.5 (0.5)	0	0	0	-
Soil characteristics						
Depth Ah-layer	5.3 (1.4)$^{a, b}$	6.9 (2.5)^{a}	5.6 (2.3)$^{a, b}$	3.1 (1.1)^{b}	n.a.	***
Litter depth (cm)	3.7 (1.6)^{a}	4.4 (1.3)^{a}	5.3 (1.4)$^{a, b}$	7.3 (3.3)^{b}	n.a.	**
C 0–5 cm (g/100g)	2.4 /1.4)^{A}	3.1 (1.1)^{A}	3.6 (2.0)^{A}	3.4 (1.3)^{A}	42.4 (0.7)^{B}	***
N 0–5 cm (g/100g)	0.1 (0.1)^{A}	0.1 (0.1)^{A}	0.2 (0.1)^{A}	0.1 (0.1)^{A}	1.0 (0.1)^{A}	***
Litter weight (g per 25 cm^2)	14 (5)^{a}	15 (6)^{a}	18 (4)^{a,b}	26 (17)^{b}	n.a.	*
pH	5.4 (0.2)^{a}	5.3 (0.2)^{a}	5.2 (0.2)^{a}	4.7 (0.5)^{b}	3.0 (0.2)^{c}	***
Diversity						
Richness	17 (4)^{a}	18 (7)^{a}	29 (5)^{b}	14 (5)^{a}	7 (2)^{c}	***
Variable damping	6.3 (0.4)^{a}	6.2 (0.4)^{a}	5.6 (0.3)^{b}	5 (0.6)^{c}	2.9 (0.2)^{d}	***
Leaf anatomy (%)						
Mesomorph	41 (5)^{A}	41 (6)^{A}	51 (3)^{B}	40 (9)^{A}	5 (8)^{D}	***
Scleromorph	56 (5)^{a}	55 (8)^{a}	36 (5)^{b}	41 (10)^{b}	64 (13)^{a}	***

Cluster A: '*Eremogone saxatilis – Pinus sylvestris*'-type

This type included dry sites with a high pH on pure sand e.g. on old dunes. It had the highest frequency of fire traces, almost the half of it was strongly burnt (Fig. 3). The field layer was rather sparse and bryophyte cover was almost absent. With high fidelity indices *Eremogone saxatilis, Polygonatum odoratum* and *Veronica spicata* are associated with this type (Table 1). In addition there are eight species such as *Carex ericetorum*, *Carex supina* and *Antennaria dioica* classified as 'character species' for type A and B.

Cluster B: '*Calamagrostis epigeios – Pinus sylvestris*'-type

The '*Calamagrostis epigeios – Pinus sylvestris*'-type was characterized by a significantly higher cover of bryophytes and a smaller amount of burnt sites than type A (Fig. 3). As it occurred on relatively dry sands as well, it had a shallow litter layer and low indicator values

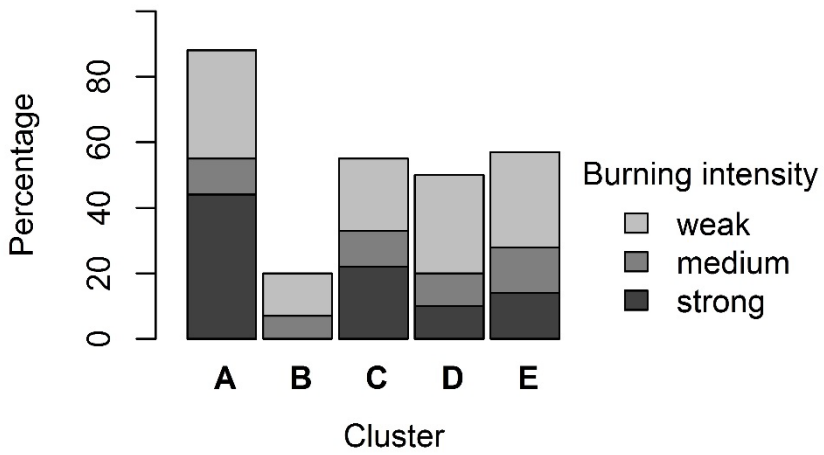

Fig. 3. Barplot showing the percentage of plots within clusters with burning intensity levels.

Abb. 3. Prozentualer Anteil und Brand-Intensität der Plots, nach Typen aufgeteilt.

for nutrients. It shares a number of species with high *Φ*-values with the Cluster A, but in addition, *Calamagrostis epigeios* is exclusively associated to this type. In contrast to the '*Eremogone saxatilis – Pinus sylvestris'*-type, bryophytes such as *Dicranum polysetum* and *Hylocomium splendens* are assigned to this group.

Because of the high proportion and abundances of *Pyroloidae*, the clusters A and B are assigned to the *Peucedano-Pinetum* W. Matuszkiewicz 1962 in the alliance *Dicrano-Pinion*, class *Vaccinio-Piceetea*.

Cluster C: '*Cnidium dubium – Pinus sylvestris*'-type

This type occurred on sandy soils with silty or loamy sand in the subsoil, which is reflected by higher nutrient and moisture levels compared with Clusters A and B (Table 2). It was moister and offered more nutrients than the types described before (Table 2). With an average of 29 species, the highest species richness per plot occurred in this type. *Cnidium dubium*, *Fragaria viridis* and *Viola montana* are associated to this type with very high fidelity indices. *Betula pendula* had a high mean cover in the tree layer occurring in two thirds of the relevés. Most of the 'character species' were mesophilous and may - such as *Cnidium dubium*, *Geranium pratense* and *Vicia sepium* - also occur commonly in open grassland habitats.

Next page (nächste Seite):

Fig. 4. a) Cluster A: '*Eremogone saxatilis – Pinus sylvestris'*-type. Scorch marks are found on the tree's bark. The field layer cover is sparse, bryophyte cover is absent; **b)** Cluster B: '*Calamagrostis epigeios – Pinus sylvestris'*-type. Bryophyte cover is high, apart from that the structure is similar to the previous type; **c)** Cluster C: '*Cnidium dubium – Pinus sylvestris'*-type. Pine is accompanied by birch, the ground vegetation is luxuriant. Competitiors such as *Pteridium aquilinum* are frequent; **d)** Cluster D: '*Calamagrostis canescens – Pinus sylvestris* -type. Dwarf shrubs such as *Vaccinium* species and

Ledum palustre dominate in these moister stands; **e)** Cluster E: '*Chamaedaphne calyculata – Pinus sylvestris'*-type. Tree height is low, ground vegetation is dominated by *Chamaedaphne calyculata* and *Ledum palustre*. *Sphagnum*-cover is near 100% and its peat forms the substrate (photos M. Freitag, 2014).

Abb. 4. a) Cluster A: '*Eremogone saxatilis – Pinus sylvestris'*-Typ. In allen Aufnahmen sind Brandspuren an den Bäumen zu finden. Die Deckung der Feldschicht ist gering, eine Bryophytenschicht nicht vorhanden; **b)** Cluster B: '*Calamagrostis epigeios – Pinus sylvestris'*-Typ. Die Struktur ist ähnlich der im vorigen Typ, allerdings ist hier eine hohe Deckung von Bryophyten zu finden; **c)** Cluster C: '*Cnidium dubium – Pinus sylvestris'*-Typ. Neben Kiefer ist sind auch Birken in der Baumschicht zu finden. Die Bodenvegetation ist wüchsig, mit konkurrenzkräftigeren Arten wie *Pteridium aquilinum;* **d)** Cluster D: '*Calamagrostis canescens – Pinus sylvestris* -Typ. Zwergsträucher wie *Vaccinium*-Arten und *Ledum palustre* dominieren diese feuchteren Standorte; **e)** Cluster E: '*Chamaedaphne calyculata – Pinus sylvestris'*-Typ. Die Baumschicht ist niedrig, die Bodenvegetation ist dominiert von *Chamaedaphne calyculata* und *Ledum palustre*. Die *Sphagnum*-Deckung ist nahezu 100% über *Sphagnum*-Torf (Fotos: M. Freitag, 2014).

Although cluster C has a high number of mesic 'character species' such as *Rubus saxatilis* indicating a transition to mesotrophic birch forests on loamy soils xero-mesophytic species such as *Chimaphila umbellata, Lupinaster pentaphyllum* and others were still highly frequent, justifying the integration into the *Peucedano-Pinetum*.

Cluster D: '*Calamagrostis canescens – Pinus sylvestris'* -type

Type D occurred in wet depressions or in the transition zone to bog pine forests. There are no exclusive 'character species' for this type. Mesophytic forest species such as *Maianthemum bifolium*, *Trientalis europaea* and *Vaccinium myrtillus* are assigned to this vegetation type, whereas the *Φ*-values of xero-mesophytic species are negative (e.g. the highly frequent *Chimaphila umbellata*, *Lupinaster pentaphyllus* and *Solidago virgaurea*). *Ledum palustre* and *Carex lasiocarpa* shared with cluster E, illustrate the floristic and ecological relatedness of these two vegetation types.

The assignment of cluster D to a specific association is less straightforward and equivocal as there was a predominance of mesophytic coniferous forest species, which gives the analysed stands a somehow intermediate position between the *Vaccinio Piceetea* and *Vaccinio uliginosae Pinetea.* However, due to the regular occurrence of typical bog species such as *Ledum palustre*, *Carex lasiocarpa* and *Calamagrostis canescens* most samples of Cluster D can be assigned to the *Vaccinio uliginosi-Pinetum sylvestris* as well.

Cluster E: '*Chamaedaphne calyculata – Pinus sylvestris'*-type

This type had the lowest cover and the lowest average height of the tree layer. It was found on bogs and in forest depressions on peat. In five out of seven relevés the peat thickness was higher than 90 cm (end of measuring scale), the minimum was 25 cm. Vascular plant species richness in this type was lowest in this study (minimum: 4, maximum: 9), whilst the proportion of stress tolerating plants was high. Five typical bog species (including *Andromeda polifolia*, *Eriophorum vaginatum* and *Oxycoccus palustris*) were exclusively associated with this type (Table 1). *Chamaedaphne calyculata* had the highest possible fidelity index, showing that it is diagnostic for this vegetation type. In the pooled *Sphagnum* samples typical ombrotrophic species such as *S. magellanicaum* and *S. angustifolium* were predominant (Supplement E2).

Cluster E can be assigned to *Vaccinio uliginosi-Pinetum sylvestris* Kleist 1929 em. Matuszkiewicz 1962 in the class *Vaccinio uliginosae Pinetea*, because of the high frequency and abundance of typical bog species such *as Chamaedaphne calyculata, Oxycoccus palustris*, *Andromeda polifolia* and *Eriophorum vaginatum* and the absence of mesophytic forest species.

As cluster E is floristically and pedo-genetically distinct from all other clusters (which is indicated by its representation as one of the two main branches in the dendrogram), we excluded it from further statistical analyses to ease the interpretation of environmental and fire effects on community structure.

4.2 Gradient analysis

The first axis of DCA ordination had a length of 3.01 SD-units (Table 3) and displayed a pronounced humidity gradient, which was negatively correlated with soil pH (Fig. 5). All clusters were distinctly ordered along this gradient. The second axis represented a gradient in bryophyte cover that is negatively correlated to species richness, the proportion of mesomor-

Table 3. Pearson's correlation coefficients (r^2) between ordination scores and environmental variables. Significance p was tested with a permutation test (1000 permutations, p-levels: 0.05 > * > 0.01 > ** > 0.001 > ***).

Tabelle 3. Pearson's Korrelationskoeffizienten (r^2) von Achsenwerten und Umweltvariablen in der DCA. Signifikanz p wurde mit einem Permutationstest getestet (1000 Permutationen, p-Level: 0,05 > * > 0,01 > ** > 0,001 > ***).

	Axis 1	**Axis 2**		
Axis length (SD)	3.01	2.18		
Eigenvalues	0.39	0.21		
	Vector's direction cosines		r^2	p
Cover bryophytes	0.11	-0.99	0.24	**
Cover field layer	0.86	0.52	0.51	***
Nutrients (ind. val.)	0.37	0.93	0.45	***
Soil humidity (inv. val.)	0.98	-0.17	0.91	***
Soil pH	-0.87	0.46	0.57	***
Richness	0.19	0.98	0.60	***
Leaf anatomy mesomorph	0.26	0.96	0.51	***
Leaf anatomy scleromorph	-0.73	-0.68	0.74	***

phic leaf anatomy and the nutrient indicator value. The latter three were all strongly intercorrelated, finding their optimum in Cluster C (Fig. 5, Table 3). Vice versa, Clusters A and B are characterized by a high proportion of species with scleromorphic leaves.

4.3 Effects of fire

We found no significant impact of burning on species richness (t-test, $p = 0.94$). However, the cover of ground-dwelling bryophytes was highly negatively correlated with fire intensity ($\rho = -0.60$, $n = 43$, $p < 0.001$).

5. Discussion

5.1 Vegetation response to site conditions

The studied pine forests had a comparatively open canopy as it is typical of hemiboreal forests. The open canopy is an important attribute of all *Pinus sylvestris* forests, supplying the ground layer vegetation with sufficient levels of light (CHYTRÝ et al. 2012, ERMAKOV 2010). Hence as in many boreal forests (LAHTI & VÄISÄNEN 1987), moisture, soil pH and fertility were the major factors for further differentiation in floristic composition and structure.

Site conditions ranged from dry sandy soils on dunes with a low groundwater table to pine-sphagnum communities on wet peat substrate in depressions, which highlights topography as the major ecological gradient on nutrient poor sand. In ordination space this is re flected by a pronounced soil pH and humidity gradient along the first DCA axis. Consistent with the description of oligotrophic pine forests (ERMAKOV et al. 2000, ERMAKOV & MAKHATKOV 2011, ERMAKOV & MOROZOVA 2011, POLYAKOVA & ERMAKOV 2008), thexero-mesophytic species *Antennaria dioica*, *Carex ericetorum*, *Carex supina*, *Chimaphi-*

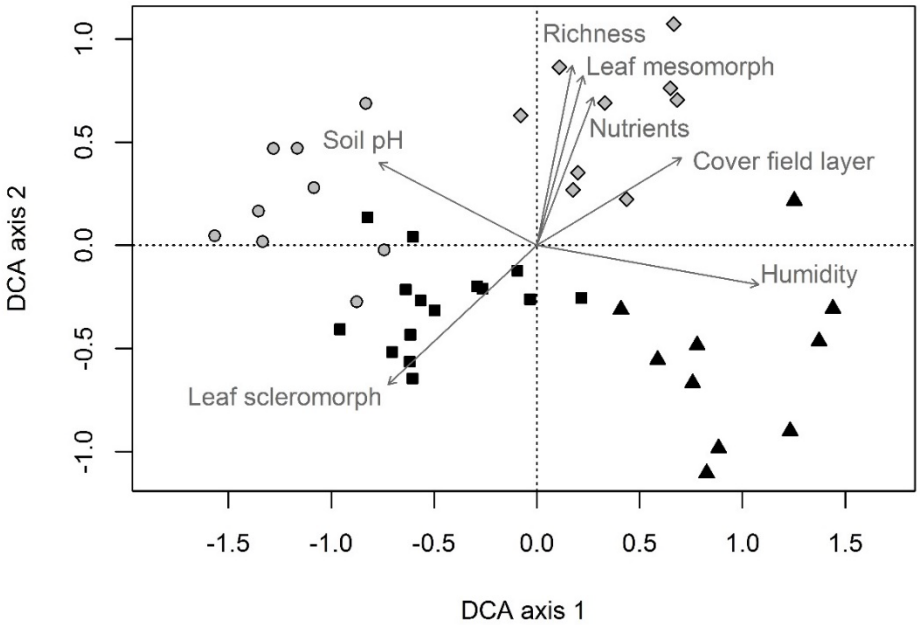

Fig. 4. DCA ordination displaying sites and correlation vectors of environmental gradients. Vegetation types were defined by hierarchical cluster analysis, but type **E** was excluded. Correlation vectors point in the direction of which projections of sites onto vectors have maximum correlation with corresponding environmental variables, their lengths are scaled by correlation coefficients. See Table 3 for further information.

Abb. 4. DCA Ordination mit Aufnahmen und Korrelationsvektoren von ausgewählten Umweltgradienten. Vegetationstypen wurden durch hierarchische Clusteranalyse gebildet, aber Typ **E** ausgeschlossen. Korrelationsvektoren zeigen in die Richtung, in der die Projektionen der Aufnahmen die höchste Korrelation mit dazugehörigen Umweltvariablen haben. Die Länge der Vektoren ist nach Größe der Korrelationskoeffizienten skaliert. Tabelle 3 enthält dazugehörige Informationen.

la umbellata and *Pyrola chlorantha* were assigned to the driest types (clusters A and B) with high fidelity values (Table 1). An increase of species with scleromorphic leaf anatomy reflects the adaption to drought stress.

With increasing humidity, the dwarf shrubs *Vaccinium myrtillus* and *Vaccinium vitis-idea* gained abundance as already observed by BEZKOROVAINAYA et al. (2007) and PEREVOZNIKOVA et al. (2007). *Ledum palustre* in the '*Calamagrostis canescens – Pinus sylvestris* -type indicates colder sandy deposits (ERMAKOV & MOROZOVA 2011), having mesophilous forest species such as *Maianthemum bifolium* with the '*Cnidium dubium – Pinus sylvestris*'-type in common. On the other hand, *L. palustre* and *Carex lasiocarpa* can also be found in peat bogs. Accordingly, the '*Calamagrostis canescens – Pinus sylvestris* -type can be characterized as an ecotonal type, containing species typical of both bogs and forests (ERMAKOV & MAKHATKOV 2011). However, the decline of soil pH towards increasing humidity acts as minor predictor for species composition on mineral soils, as low pH in wetter soils are just a side effect of more intense soil leaching under wetter conditions (CHYTRÝ et al. 2007).

Species-richness was lowest under particularly dry or wet nutrient-poor conditions and increased towards mesic moisture and nutrient levels. The mean soil humidity indicator values implied a unimodal relationship between richness and moisture.

Pine forests in the study area represent a vegetation type growing on sites with extreme environmental conditions not only in terms of humidity. Because of the sandy substrate, there are few colloidal particles which adsorp cations. This favours the downward migration of nutrients set free by decomposition of litter (BEZKOROVAINAYA et al. 2007). In most of the '*Cnidium dubium – Pinus sylvestris'*-type plots, we have found clayey substrate below a shallow layer of pure sand. Nutrient leaching was lower under these conditions so that birch frequency and cover was higher in this type (see also Supplement E2) as birch can compete with pine on clayey soils (BLYAKHARCHUK 2003). Besides the occurrence of birch, an increasing amount of species with mesomorphic leaves and increasing productivity (as expressed cover of the field layer) indicated higher water and nutrient supply due to the soil substrate's higher water holding capacity.

Compared to pine forests, birch forests have a higher diversity (ERMAKOV et al. 2000, GOTTBEHÜT 2013). PEKIN et al. (2012) found the highest species richness in forests, where dominant species are nutrient-limited. As there is a positive relationship between species richness and nutrient supply in this study, dominant species in pine forests must still be nutrient-limited. This favours the appearance of pure stress-tolerators (e.g. *Orthilia secunda*) as well as competitors (e.g. *Pteridium aquilinum*) side-by-side in the species-richest '*Cnidium dubium – Pinus sylvestris'*-type (KLOTZ et al. 2002, ROSENZWEIG & ABRAMSKY 1993). Therefore *Betula pendula* forests in the study area exhibit a larger species pool due to higher soil fertility and better moisture supply, which is reflected in the '*Cnidium dubium – Pinus sylvestris'*-type by a particularly high number of characteristic species. Many of these such as *Galium boreale*, *Cnidium dubium* and *Rubus saxatilis* are common in birch forests in the study area (GOTTBEHÜT 2013, NIMIS et al. 1994), indicating the transitional character of the '*Cnidium dubium – Pinus sylvestris'*-type to birch forests.

The '*Chamaedaphne calyculata – Pinus sylvestris'*-type is floristically separated from all other types (e.g. see Fig. 2) by pure stock of typical bog plants. This type occurs in bogs all over the Holarctic. Due to very low pH (mean pH: 3.0), there are only a few specialist plants able to grow under such harsh conditions.

5.2 Effects of fire

Fire has an eminent effect shaping the tree canopy as well as the ground vegetation structure of pine forests (WIRTH 2005). In our study, the correlation between fire intensity and bryophyte cover was negative, that is, low and medium fire intensities affected the bryophyte layer less than high fire intensities. Contrary to this correlation, BEZKOROVAINAYA et al. (2007) found a fully destroyed bryophyte-lichen cover without any impact of fire intensity. *Dicranum polysetum* and *Pleurozium schreberi* in their study started to recover 5 years after a fire, overall bryophyte cover was fully restored after 10 years. We assume, that vanishing scorch marks couldn't be distinguished from low severity scorch marks, so that the estimate of fire intensity in this study did not only represent intensity but also the time passed since the last fire event. The assignment of the moss species *D. polysetum*, *Hylocomium splendens* and *P. schreberi* to the '*Calamagrostis epigeios – Pinus sylvestris'*-type shows a clear differentiation of dry pine forest types due to fire, with the '*Eremogone saxatilis – Pinus sylvestris'*-type as an early stage in post-fire-succession.

In contrast to MAROZAS et al. (2007), we found no significant difference in vascular plant species richness between burnt and unburnt sites. There are two possible explanations for this. First, the removal of litter and understory vegetation does not play such an important role, since the litter layer thickness and the cover of understory vegetation are per se low in the dry and unproductive pine forests of the study region. Moreover, the nitrogen compounds set free by fire vanish within two years (BEZKOROVAINAYA et al. 2007). Hence, the repression of dominant species by fire is more important in productive forests, where competition is limiting species richness. Second, it could be that the positive effect of litter and understory removal lasts longer than scorch marks can be noticed on the tree's bark. A surface fire removes between 10% and 50% of the litter layer (CONARD & IVANOVA 1997). The development of thick litter layers takes about 100 years (GORSHKOV et al. 1996), which could be the reason for the almost equal litter layer thickness of the '*Eremogone saxatilis – Pinus sylvestris*'- and '*Calamagrostis epigeios – Pinus sylvestris*'-types in this study. Anyway, the '*Eremogone saxatilis – Pinus sylvestris*'-type is slightly drier than the '*Calamagrostis epigeios – Pinus sylvestris*'-type (Table 2), which can be a consequence of higher evaporation due to a temporally shallower litter layer and removed bryophyte-carpet.

Furthermore, the species *Eremogone saxatilis*, *Polygonatum odoratum* and *Veronica spicata* seem to be inhibited by the bryophyte layer, as they are clear 'character species' of the burnt *'Eremogone saxatilis – Pinus sylvestris'*-type. Possibly, they benefit from the shallower litter layer and removed bryophyte-carpet, making it easier to reach the mineral soil and establish successfully.

5.3 Regional comparison

The floristic composition of the dry pine forest types (Cluster A–C) shows a considerable overlap with continental European *Peucedano-Pinetum* communities (Supplement S1). Those communities are heavily tied to slightly acidified, dry and unproductive habitats (HEINKEN 2008b). The per se rare habitats sharply declined in Germany during the previous century due to abandonment of forest pasture or litter raking, acidification and atmospheric nitrogen inputs (HEINKEN 2008a, PRIETZEL & KAISER 2005, REINECKE et al. 2014), so that they are near to disappearance. In contrast, MATUSZKIEWICZ et al. (2013) found *Chimaphila umbellata*, *Pyrola chlorantha* and *Orthilia secunda* even in recent pine forests on former agricultural fields on sandy, podzolic soils in North-Eastern Poland. These initial development stages offer conditions comparable to those under the climate of the Western Siberian Pre-Taiga where organic layers are regularly removed by fires. Characteristic species for the *Peucedano-Pinetum* such as *Chimaphila umbellata*, *Pyrola chlorantha*, *Carex ericetorum*, *Viola rupestris*, *Goodyera repens* and *Polygonatum odoratum* (HEINKEN 2008b) had considerably higher fidelity in Western Siberia and Poland. Furthermore, these characteristic *Peucedano-Pinetum* species are also common further to the east in pine forest of South Central Siberia (POLYAKOVA & ERMAKOV 2008).

Differences regarding the distribution range of European species are most apparent in the lack of several shrubs and deciduous tree species such as *Quercus robur* and characteristic herbaceous species such as *Peucedanum oreoselinum* or *Anthericum ramosum*. However, in comparison with pine forest of South Central Siberia (POLYAKOVA et al. 2008; POLYAKOVA & ERMAKOV 2008), a wide range of species with an Asian distribution are missing as well. Among the regularly occurring species in our samples, only *Dianthus versicolor* and *Lupinaster pentaphyllus* have their main distribution in Asia. Overall, these patterns clearly high-

light the much stronger similarity of the studied Western Siberian pine forests with communities from Central Europe giving further evidence to the phytogeographic concept of a 'Euro-Siberian Vegetation circle'.

A striking difference with regard to site conditions is the lack of subatlantic acidophilous species such as *Deschampsia flexuosa* or *Veronica officinalis* in the dry pine forest types (11–13; Cluster A–C). Due to the rather dry climatic conditions in Siberia topsoil acidification by the leaching of base cations is retarded, which is reflected in the soil profiles by relatively high pH-values of around five and a rather cryptic podzolization. This is also indicated by species typical of dry calcareous forest such as *Lathyrus vernus*. Recurring light surface fires, which limit litter accumulation, and dry conditions on nutrient-poor soils enable low-competitive species to dominate. Hence, a peculiarity of the Siberian dry forests is the high frequency of typical xero-mesophytic meadow-steppe species (POLYAKOVA & ERMAKOV 2008) such as *Eremogene saxatilis*, *Carex supina*, *Lupinaster pentaphyllus* or *Veronica spicata*. Under the given site conditions and disturbance regimes the oligotrophic pine forests in Western Siberia are a (pyro-) climax community, while in Europe these communities are rather short-lived successional stages that depend on a specific forest management (BEER & EWALD 2005).

A major advice from our study for conservation management is that rather crude measures counteracting the accumulation of organic layers such as regular ground fires or sod-cutting are mandatory to maintain *Pyroloidae*-rich Pine forests. In Central Europe, with high levels of atmospheric nitrogen deposition, such regular disturbances are even more crucial. Vice versa the absence of pollution in Western Siberia was clearly indicated by species assemblages purely dominated by oligotrophic, stress-tolerant species.

Erweiterte deutsche Zusammenfassung

Einleitung - Hemiboreale (boreonemorale) Wälder sind in West-Sibirien in der Übergangszone zwischen Sub-Taiga im Norden und Wald-Steppe im Süden zu finden (ERMAKOV et al. 2000). Aufgrund des humiden, stark kontinentalen Klimas dominieren lichtbedürftige Baumarten wie *Betula pendula et pubescens*, *Populus tremula* und *Pinus sylvestris*. Wegen ihrer offenen Kronen-Struktur ist die Bodenvegetation sehr artenreich. Ein Großteil der Arten ist ebenfalls in West- und Mitteleuropa verbreitet (ERMAKOV & MOROZOVA 2011), was durch den Begriff ‚eurosibirischer Vegetationskreis' verdeutlicht wird. Von *Pinus sylvestris* dominierte Wälder kommen wie in Europa auf azonalen Sandböden natürlich vor, wie sie vor allem an den Terrassen großer Flüsse zu finden sind. Diese Standorte sind sehr trocken und nährstoffarm, außerdem sind schwache Oberflächenfeuer ein häufiges Phänomen. Allerdings sind diese Wälder im Vergleich zu mesischen Standorten nur wenig untersucht.

Methoden - Im Juni und Juli 2014 wurden 50 Vegetationsaufnahmen in von *Pinus sylvestris* dominierten Wäldern auf Mineral- sowie auf Torfböden entlang der Flüsse Tura und Tobol im Oblast Tyumen (Abb. 1) durchgeführt. Auf 100 m² wurden alle Gefäßpflanzenarten, Moose und Flechten notiert und ihre Deckung geschätzt (VAN DER MAAREL 1979). Moose und Flechten konnten zum Teil nur auf Gattungs-Niveau bestimmt werden. Zusätzlich wurden Boden-, Struktur- und Brandparameter aufgenommen (Tab. 2). Aus den Vegetationsaufnahmen wurden mit hierarchischer Clusteranalyse (Methode ‚flexible beta') fünf Vegetationstypen abgegrenzt (Abb. 2). Für die Typen wurden mit dem *phi coefficient of association* (TICHÝ & CHYTRÝ 2006) diagnostische Arten ermittelt. Die Beziehung zwischen Umweltgradienten und Artenzusammensetzung wurde mit einer DCA untersucht.

Ergebnisse - Insgesamt wurden 105 Gefäß-, 10 Moos- und 5 Flechtenarten erfasst. Die mittlere Artenzahl pro Aufnahme lag bei 22 (Minimum: 9; Maximum: 43). Die Artenzusammensetzung der Vegetationstypen (Tab. 1) wurde in erster Linie durch die Bodenfeuchte bestimmt. Folglich bildeten die

Typen einen Gradienten von sehr trockenen, oligotrophen Standorten auf Krypto-Podsolen mit geringer Humusauflage bis hin zu niedrigwüchsigen Kiefernwäldern im Randbereich ombrotropher Hochmoore. Die bessere Wasser- und Nährstoffverfügbarkeit in Böden mit lehmigen Sanden um Unterboden führte zu höherer Produktivität und Diversität der Feldschicht (Abb. 5). Oberflächenfeuer, natürlich oder anthropogen verursacht, entfernten die Moosschicht nahezu völlig.

Diskussion - Bodenfeuchte, Nährstoffe und Feuer sind die drei bestimmenden Umweltfaktoren in oligotrophen Kiefernwäldern im südlichen West-Sibirien. Die feuchtesten Standorte sind Moor-Kiefernwälder der Klasse *Vaccinio uliginosae Pinetea* Passarge et G. Hofmann 1968 mit moortypischen, circumboreal verbreiteten Arten. Auf sehr trockenen, nährstoffarmen Sanden bildet sich eine Wärme und Trockenheit liebende Pflanzengesellschaft aus mit Arten wie *Chimaphila umbellata*, *Solidago virgaurea* und einem großen Anteil von *Pyroloideaen* (ERMAKOV et al. 2000). Die nährstoffreicheren Ausbildungen weisen einen höheren Anteil mesischer Arten wie *Cnidium dubium* und *Rubus saxatilis* auf und stellen den Übergang zu *Betula pendula* dominierten Wäldern dar. Diese Gesellschaften werden durch wiederkehrende, schwache Oberflächenfeuer offen gehalten, sodass die Humusauflage gering bleibt und konkurrenzkräftigere Arten wie *Vaccinium* spp. zurückgedrängt werden. In Struktur und Artenzusammensetzung sind sie ähnlich zum *Peucedano Pinetum* W. Matuszkiewicz 1962 (Beilage S1), das in Mitteleuropa wegen hoher Stickstoffimmissionen und Streuakkumulation nur noch reliktisch zu finden ist (HEINKEN 2008a, REINECKE et al. 2014). Für den Naturschutz bedeutet dies, dass die Erhaltung von *Pyroloidae*-reichen Kiefernwäldern nur durch grobe Maßnahmen wie regelmäßige Bodenfeuer oder Streurechen möglich ist.

Acknowledgements

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Supplements

Supplement S1. Frequency table of species in different pine forest communities of Germany (1–5), Poland (6–10), South Western Siberia (11–13) and South Central Siberia (14–16).

Beilage S1. Übersichtstabelle von häufigen Arten in verschiedenen Kiefernwäldern Deutschlands (1–5), Polens (6–10), Südwest Sibiriens (11–13) und Zentralsibiriens (14–16).

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

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

Supplement E1. Floristic composition and environmental determinants of pine forests (all relevés, $n = 50$) in the hemiboreal zone of Western Sibiria.

Anhang E1. Artenzusammensetzung und Umweltdeterminanten von Kiefernwäldern (alle Vegetationsaufnahmen, $n = 50$) der hemiborealen Zone Westsibierens.

Supplement E2. Complete list of all observed species in the all relevés ($n = 50$).

Anhang E2. Vollständige Artenliste der Vegetationsaufnahmen ($n = 50$).

References

ADÁMEK, M., BOBEK, P., HADINCOVÁ, V., WILD, J., & KOPECKÝ, M. (2015): Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. – For. Ecol. Manag. 336: 81–90.

BEER, A. & EWALD, J. (2005): Vegetationskundliche Untersuchungen rezent streugenutzter Kiefernwälder auf Binnendünen des niederbayerischen Tertiärhügellandes. – Tuexenia 25: 93–109.

BEZKOROVAINAYA, I.N., TARASOV, P.A., IVANOVA, G.A., BOGORODSKAYA, A.V. & KRASNOSHCHEKOVA, E.N. (2007): The nitrogen reserves in sandy podzols after controlled fires in pine forests of Central Siberia. – Eurasian Soil Sci. 40: 700–707.

BLYAKHARCHUK, T.A. (2003): Four new pollen sections tracing the Holocene vegetational development of the southern part of the West Siberian Lowland. – Holocene 13: 715–731.

CHYTRÝ, M., DANIHELKA, J., ERMAKOV, N., HÁJEK, M., HÁJKOVÁ, P., KOČÍ, M., KUBEŠOVÁ, S., LUSTYK, P., OTÝPKOVÁ, Z., POPOV, D., ROLEČEK, J., ŘEZNÍČKOVÁ, M., ŠMARDA, P. & VALACHOVIČ, M. (2007): Plant species richness in continental southern Siberia: effects of pH and climate in the context of the species pool hypothesis. – Glob. Ecol. Biogeogr. 16: 668–678.

CHYTRÝ, M., DANIHELKA, J., HORSÁK, M., KOČÍ, M., KUBEŠOVÁ, S., LOSOSOVÁ, Z., OTÝPKOVÁ, Z., TICHÝ, L., MARTYNENKO, V.B. & BAISHEVA, E.Z. (2010): Modern analogues from the Southern Urals provide insights into biodiversity change in the early Holocene forests of Central Europe. – J. Biogeogr. 37: 767–780.

CHYTRÝ, M., DANIHELKA, J., KUBEŠOVÁ, S., LUSTYK, P., ERMAKOV, N., HÁJEK, M., HÁJKOVÁ, P., KOČÍ, M., OTÝPKOVÁ, Z., ROLEČEK, J., ŘEZNÍČKOVÁ, M., ŠMARDA, P., VALACHOVIČ, M., POPOV, D. & PIŠÚT, I. (2008): Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. – Plant Ecol. 196: 61–83.

CHYTRÝ, M., ERMAKOV, N., DANIHELKA, J., HÁJEK, M., HÁJKOVÁ, P., HORSÁK, M., KOČÍ, M., KUBEŠOVÁ, S., LUSTYK, P., OTÝPKOVÁ, Z., PELÁNKOVÁ, B., VALACHOVIČ, M., ZELENÝ, D. & HUSTON, M. (2012): High species richness in hemiboreal forests of the northern Russian Altai, southern Siberia. – J. Veg. Sci. 23: 605–616.

CONARD, S.G. & A. IVANOVA, G.A. (1997): Wildfire in Russian boreal forests - potential impacts of fire regime characteristics on emissions and global carbon balance estimates. – Environ. Pollut. 98: 305–313.

CZEREPANOV, S.K. (1995): Vascular plants of Russia and adjacent states (the former USSR). – Cambridge University Press, New York: 528 pp.

DE CÁCERES, M. & LEGENDRE, P. (2009): Associations between species and groups of sites: indices and statistical inference. – Ecology 90: 3566–3574.

DE CÁCERES, M., LEGENDRE, P. & MORETTI, M. (2010): Improving indicator species analysis by combining groups of sites. – Oikos 119: 1674–1684.

DIDUKH, Y.P. (2011): The ecological scales for the species of Ukrainian flora and their use in synphytoindication. – Phytosociocentre, Kiev. 176 pp.

ERMAKOV, N. (2010): Corresponding geographical types of hemiboreal forests in North Asia: peculiarities of ecology and genesis. – Phytocoenologia 40: 29–40.

ERMAKOV, N., DRING, J. & RODWELL, J. (2000): Classification of continental hemiboreal forests of North Asia. – Braun-Blanquetia 28: 1–131.

ERMAKOV, N. & MAKHATKOV, I. (2011): Classification and ordination of north boreal light-coniferous forests of the West Siberian Plain. – Plant Biosyst. 145: 199–207.

ERMAKOV, N. & MOROZOVA, O. (2011): Syntaxonomical survey of boreal oligotrophic pine forests in northern Europe and Western Siberia. – Appl. Veg. Sci. 14: 524–536.

ESSLINGER, T.L. (2014): A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada (Version 19). – URL: http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm [accessed 2014–08–28].

GLOBAL ADMINISTRATIVE AREAS (2012): GADM database of Global Administrative Areas, version 2.0. – URL: http://www.gadm.org [accessed 201–03–24].

GORSHKOV, V.V., BAKKAL, I.J. & STAVROVA, N.I. (1996): Postfire recovery of forest litter in Scots pine forests in two different regions of boreal zone. – Silva Fenn. 30: 209–219.

GOTTBEHÜT, K. (2013): Birch forests in Western Siberia - a modern analogue to pre-boreal European forests. – Master's thesis, Münster: 23 pp.

HEINKEN, T. (2008a): Die natürlichen Kiefernstandorte Deutschlands und ihre Gefährdung. – Beitr. Nordwestdtsch. Forstl. Versuchsanst. 2: 19–41.

HEINKEN, T. (2008b): *Vaccinio-Piceetea* (H7). Beerstrauch-Nadelwälder. Teil 1: *Dicrano-Pinion*. – Sand- und Silikat-Kiefernwälder. – Synopsis Pflanzenges. Dtschl. 10: 1–88.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. (2001): TurboVeg, a comprehensive data base management system for vegetation data. – J. Veg. Sci. 12: 589–591.

IGNATOV, M.S., AFONINA, O.M. & IGNATOVA, E.A. (2006): Check-list of mosses of East-Europe and North-Asia. – Arctoa 15: 1–130.

JUPP, T.E., TAYLOR, C.M., BALZTER, H. & GEORGE, C.T. (2006): A statistical model linking Siberian forest fire scars with early summer rainfall anomalies. – Geophys. Res. Lett. 33: L14701.

KLOTZ, S., KÜHN, I. & DURKA, W. (2002): BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. – Schriftenr. Vegetationskd. 38: 1–334.

LAHTI, T. & VÄISÄNEN, R.A. (1987): Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. – Vegetatio 68: 145–156.

MAECHLER, M., ROUSSEEUW, P., STRUYF, A., HUBERT, M., HORNIK, K., STUDER, M. & ROUDIER, P. (2014): cluster: Cluster Analysis Basics and Extensions. R package version 1.15.2.

MAROZAS, V., RACINSKAS, J. & BARTKEVICIUS, E. (2007): Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. – For. Ecol. Manag. 250: 47–55.

MATUSZKIEWICZ, J.M., KOWALSKA, A., KOZŁOWSKA, A., ROO-ZIELIŃSKA, E. & SOLON, J. (2013): Differences in plant-species composition, richness and community structure in ancient and post-agricultural pine forests in central Poland. – For. Ecol. Manag. 310: 567–576.

MATUSZKIEWICZ, W. & MATUSZKIEWICZ, J. (1973): Przegląd fitosocijologiczny zbiorowisk leśnych Polski. Cz. II. Bory Sosnowe. (Phytosociological review of the forest communities of Poland: Part 2. Pine forests) [in Polish]. – Phytocoenosis 4: 273–356.

NIMIS, P.L., MALYSHEV, L.I. & BOLOGNINI, G. (1994): A phytogeographic analysis of birch woodlands in the southern part of West Siberia. – Vegetatio 113: 25–39.

NUZZO, V.A., MCCLAIN, W. & STROLE, T. (1996): Fire impact on groundlayer flora in a sand forest 1990–1994. – Am. Midl. Nat. 136: 207.

OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H. & WAGNER, H. (2013): vegan: community ecology package. R package version 2.0-10.

OLSON, D.M., DINERSTEIN, E., WIKRAMANAYAKE, E.D., BURGESS, ND., POWELL, G.V.N., UNDERWOOD, E.C., D'AMICO, J.A., ITOUA, I., STRAND, H.E., MORRISON, J.C., LOUCKS, C.J., ALLNUTT, T.F., RICKETTS, T.H., KURA, Y., LAMOREUX, J.F., WETTENGEL, W.W., HEDAO, P. & KASSEM, K.R. (2001): Terrestrial Ecoregions of the World: A New Map of Life on Earth. – BioScience 51: 933–938.

PEKIN, B.K., BOER, M.M., WITTKUHN, R.S., MACFARLANE, C., GRIERSON, P.F. & ROXBURGH, S. (2012): Plant diversity is linked to nutrient limitation of dominant species in a world biodiversity hotspot. – J. Veg. Sci. 23: 745–754.

PEREVOZNIKOVA, V.D., IVANOVA, G.A., IVANOV, V.A. & KOVALEVA, N.M. (2007): Transformation of ground vegetation under the effect of fires in pine forests of Middle Siberia. – Russ. J. Ecol. 38: 444–448.

POLYAKOVA, M.A., DITS, L.Y. & ERMAKOV, N. (2008): Studies on Biological Features of Band Pine Forests in the Intermontane Minusinsk Depression by Methods of Gradient Analysis. – Russ. J. Ecol. 39: 238–245.

POLYAKOVA, M.A. & ERMAKOV, N. (2008): Klassifikacija sosnovyh lesov borovyh lent Minusinskojmezhgornoj kotloviny, juzhnaja Sibir' (Classification of pine forests on sandy deposits in the Minusinskaya intermountain basin, southern Siberia) [in Russian].– Veg. Russ. 13: 82–105.

PRIETZEL, J. & KAISER, K.O. (2005): De-eutrophication of a nitrogen-saturated Scots pine forest by prescribed litter-raking. – J. Plant Nutr. Soil Sci. 168: 461–471.

R CORE TEAM (2014): R: A language and environment for statistical computing. Version 3.0.3. – R Foundation for Statistical Computing, Vienna.

REINECKE, J., KLEMM, G. & HEINKEN, T. (2014): Vegetation change and homogenization of species composition in temperate nutrient deficient Scots pine forests after 45 yr. – J. Veg Sci. 25: 113–121.

RENNWALD, E. (2000): Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. – Schriftenr. Vegetationskd. 35: 1–800.

ROSENZWEIG, M.L. & ABRAMSKY, Z. (1993): How are diversity and productivity related. – In: RICKLEFS, R.E. & SCHLUTER, D. (Eds.): Species diversity in ecological communities. Historical and geographical perspectives: 52–65. University of Chicago Press, Chicago.

RUSSIAN FEDERAL SERVICE FOR HYDROMETEOROLOGY AND ENVIRONMENTAL MONITORING: Weather information for Tyumen. Via: World Meteorological Organisation. – URL: http://worldweather.wmo.int/en/city.html?cityId=1001 [accessed 2014–08–08].

SELEZNEVA, N.S. (1973): Lesostep' (Forest steppe). – In: GVOZDETSKIY, I.A. (Ed.): Fiziko-geografičeskoe rajonirovanie Tjumenskoj oblasti (Physical geography of the Oblast Tyumen) [in Russian]: 144–174. Moscow State University, Moscow.

SHENG, Y., SMITH, L.C., MACDONALD, G.M., KREMENETSKI, K.V., FREY, K.E., VELICHKO, A.A., LEE, M., BEILMAN, D. W. & DUBININ, P. (2004): A high-resolution GIS-based inventory of the west Siberian peat carbon pool. – Glob. Biogeochem. Cycl. 18: GB3004.

SPRIBILLE, T. & CHYTRÝ, M. (2002): Vegetation surveys in the circumboreal coniferous forests: A review. – Folia Geobot. 37: 365–382.

TICHÝ, L. & CHYTRÝ, M. (2006): Statistical determination of diagnostic species for site groups of unequal size. – J. Veg. Sci. 17: 809–818.

VAN DER MAAREL, E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – Vegetatio 39: 97–114.

WAGNER, A. & WAGNER, I. (2007): Moorwälder: Kennarten und syntaxonomische Stellung. – Ber. Reinhold-Tüxen-Ges.: 163–173.

WIRTH, C. (2005): Fire regime and tree diversity in boreal forests: implications for the carbon cycle. – In: SCHERER-LORENZEN, M., KÖRNER, C. & SCHULZE, E.-D. (Eds.): Forest diversity and function. Temperate and boreal systems: 309–346. Springer, Berlin.

WISSKIRCHEN, R. & HAEUPLER, H. (1998): Standardliste der Farn- und Blütenpflanzen Deutschlands. – Ulmer, Stuttgart: 765 pp.

ZAKH, V.A., RYABOGINA, N.E. & CHLACHULA, J. (2010): Climate and environmental dynamics of the mid- to late Holocene settlement in the Tobol–Ishim forest-steppe region, West Siberia. – Quart. Int. 220: 95–101.

Supplement S2. Frequency table of species in different pine forest communities of Germany (1-5), Poland (6-10), South Western Siberia (11-13) and South Central Siberia (14-16). Species are sorted by structural layer, then arranged by frequency in the different regions. Only species with frequency >I were considered. Note that some species from German or Siberian communities not displayed for Poland may occur here with low frequencies (≤1). For number 14-16 only species shared with communities 1-13 were considered. Species not occurring in Tyumen Oblast (Western Siberia, Russia) are marked in bold. Species not or rarely occurring in Germany or Poland highlighted in grey.

Anhang S2. Übersichtstabelle von häufigen Arten in verschiedenen Kiefernwäldern Deutschlands (1-5), Polens (6-10), Südwest Sibiriens (11-13) und Zentralsibiriens (14-16). Arten wurden erst nach Strukturschicht, dann nach Häufigkeit in den verschiedenen Regionen sortiert. Es wurden nur Arten mit einer Stetigkeit >I berücksichtigt. Es ist zu beachten, dass eine Reihe von Arten der deutschen und sibirischen Gesellschaften, für die in Polen keine Eintragungen vorhanden sind, hier mit geringen Stetigkeiten (≤1) vorkommen dürften. Für Nummer 14-16 wurden nur gemeinsame Arten mit Nummer 1-13 berücksichtigt. Arten die nicht im Oblast Tyumen (Russland) vorkommen sind fettgedruckt. Arten die nicht oder nur sehr selten in Deutschland oder Polen vorkommen sind grau hervorgehoben.

1-5 HEINKEN (2008): *Peucedano-Pinetum*
1= *ligustretosum* , 2= *callunetosum,* vicariant *Vaccinium myrtillus,* 3= *callunetosum,* vicariant *Vaccinium vitis-idaea-V. myrtillus* , 4= *callunetosum,* vicariant *Picea abies -V. myrtillus* 5= *callunetosum* , vicariant without differential species

6-10 MATUSZKIEWICZ & MATUSZKIEWICZ (1973): *Peucedano-Pinetum*
6= *pulsatilletosum* , sarmatic race, 7= *pulsatilletosum* , subboreal race, 8= *typicum* , sarmatic race, 9= *typicum* , subboreal race, 10 = *typicum* , subboreal race;

11-13 this study
11= '*Eremogone saxatilis – Pinus sylvestris* '-type, 12= '*Calamagrostis epigeios – Pinus sylvestris* '-type, 13= '*Cnidium dubium – Pinus sylvestris* '-type;

14-16 POLYAKOVA et al. (2008), POLYAKOVA & ERMAKOV (2008)
14= *Oxytropido–Pinetum* var. *Caragana arborescens* , 15= *Oxytropido–Pinetum sylvestris* 16= *Ptilio–Pinetum*

Community-Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
N	15	25	40	27	42	32	72	153	170	123	9	15	9	8	24	24
Country	DE	DE	DE	DE	DE	PL	PL	PL	PL	PL	RU	RU	RU	RU	RU	RU
	Frequency															
Trees																
Pinus sylvestris	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V
Betula pendula	+	II	II	I	r	r	II	II	II	IV	.	I	III	III	II	II
Quercus robur	IV	I	II	III	V	+	.	+	r	+	.	.	.	.	.	.
Populus tremula	.	.	II	I	.	.	r	.	r	+	.	.	.	.	I	I
Picea abies	.	.	.	III	.	.	III	+	IV	V	.	.	.	.	.	.
Fagus sylvatica	II	I	r	II	II	.	.	.	.	.	.	.	.	.	.	.
Acer pseudoplatanus	II	.	+	r	r	.	.	.	.	.	.	.	.	.	.	.
Tilia cordata	I	.	r	.	II	.	.	.	.	.	.	.	.	.	.	.
Carpinus betulus	.	I	.	r	II	.	.	.	.	.	.	.	.	.	.	.
Juglans regia	II	.	r	.	+	.	.	.	.	.	.	.	.	.	.	.
Acer platanoides	+	.	II	r	.	.	.	.	.	.	.	.	.	.	.	.
Shrubs																
Sorbus aucuparia	.	IV	IV	II	r	II	III	III	V	V	.	I	III	.	.	.
Frangula alnus	.	III	III	II	.	III	III	IV	III	IV	.	I	I	.	.	.
Juniperus communis	.	+	I	+	.	V	V	V	V	III	.	.	.	.	.	.
Rosa canina	I	I	II	r	r	.	.	.	.	.	.	.	.	.	.	.
Ligustrum vulgare	IV	+	+	r	+	.	.	.	.	.	.	.	.	.	.	.
Crataegus monogyna	II	+	II	r	III	.	.	.	.	.	.	.	.	.	.	.
Corylus avellana	.	r	+	I	r	.	.	.	.	.	.	.	.	.	.	.
Berberis vulgaris	II	.	.	II	r	.	.	.	.	.	.	.	.	.	.	.
Mahonia aquifolium	+	+	II	.	.	.	.	.	.	.	.	.	.	.	.	.
Cytisus scoparius	.	.	+	III	IV	.	.	.	.	.	.	.	.	.	.	.
Sambucus nigra	II	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lonicera xylosteum	III	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Viburnum lantana	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Field layer																
Orthilia secunda	+	II	II	II	r	+	+	III	II	III	III	V	V	V	IV	V
Chimaphila umbellata	I	I	II	II	I	IV	III	II	III	III	V	V	V	III	III	IV
Carex ericetorum	II	.	III	II	III	IV	III	III	II	+	V	V	III	II	IV	I
Polygonatum odoratum	III	r	I	I	+	V	III	III	II	II	V	III	III	III	V	IV
Dicranum polysetum	III	I	+	IV	I	V	V	V	V	V	II	V	II	V	V	III
Hylocomium splendens	+	.	+	IV	I	V	V	V	V	V	.	IV	III	V	IV	V
Pleurozium schreberi	V	III	V	V	V	V	V	V	V	V	III	V	IV	V	V	V
Antennaria dioica	.	.	+	II	r	II	II	+	+	r	V	IV	III	II	IV	III
Hieracium umbellatum	I	.	II	II	II	I	I	+	+	+	V	V	IV	III	V	III
Pyrola chlorantha	+	I	II	II	I	.	II	r	I	I	IV	III	III	II	III	III
Solidago virgaurea	.	+	II	I	III	V	IV	IV	III	V	V	V	V	II	III	III
Vaccinium vitis-idaea	.	.	IV	II	.	V	V	V	V	V	II	II	V	V	IV	V
Vaccinium myrtillus	.	III	III	III	.	IV	V	V	V	V	I	II	IV	.	.	II
Calamagrostis epigeios	IV	IV	IV	I	II	IV	IV	I	I	r	III	V	II	.	I	.
Goodyera repens	I	+	.	I	r	.	II	.	II	III	II	III	I	III	III	II
Pteridium aquilinum	.	r	+	.	.	r	r	II	I	IV	.	I	III	.	.	III
Cladonia rangiferina	.	.	+	r	.	III	IV	I	+	r	.	.	.	.	II	I
Cladonia arbuscula	.	r	.	r	.	II	III	I	r	.	.	I	.	.	III	.
Viola rupestris	III	.	.	I	II	.	.	.	.	.	III	III	III	II	III	I
Galium verum	II	I	II	I	I	.	.	.	.	.	.	I	I	.	I	r
Calluna vulgaris	I	II	IV	IV	IV	V	V	V	IV	IV	I	I	I	.	.	.
Festuca ovina agg. (WSIB. *F. rupicola)*	II	IV	IV	IV	V	V	V	V	V	IV	I	I	.	.	.	.
Viola canina et *riviniana (*WSIB: *V. montana)*	III	III	III	I	IV	II	II	II	II	III	.	I	IV	.	.	.
Agrostis capillaris	II	III	III	II	II	.	I	III	+	+	I	I	II	.	.	.
Luzula pilosa	.	I	I	II	I	IV	V	IV	V	V	I	I	II	.	.	.
Melampyrum pratense	.	II	III	III	IV	V	V	V	V	IV	.	II	IV	.	.	.
Hieracium pilosella	II	III	IV	IV	IV	V	IV	IV	II	I	I	.	.	.	.	.
Dryopteris carthusiana	+	I	+	.	.	r	.	II	I	II	.	I	II	.	.	.
Achillea millefolium	+	II	I	.	II	.	.	.	.	.	I	I	III	.	.	.
Pimpinella saxifraga	II	I	+	III	II	.	.	.	.	.	.	I	II	.	.	.
Silene nutans	I	.	.	II	I	.	.	.	.	.	II	I	III	.	.	.
Pyrola rotundifolia	.	.	.	I	.	.	.	.	r	r	.	I	III	.	.	.
Fragaria vesca	V	II	IV	II	I	III	III	III	III	III	.	.	.	V	IV	IV
Pulsatilla patens	.	.	.	+	.	IV	IV	+	+	r	IV	IV	III	I	IV	III
Calamagrostis arundinacea	.	r	.	r	.	IV	III	III	V	V	IV	IV	V	II	III	V
Maianthemum bifolium	+	+	.	+	.	.	r	I	I	IV	I	II	V	IV	III	V
Equisetum hyemale	.	.	.	r	.	.	II	r	r	r	III	IV	I	III	II	III
Rubus saxatilis	.	.	r	r	.	II	+	II	II	IV	.	III	V	V	III	V
Anthoxanthum odoratum	I	I	II	II	IV	I	I	II	I	+	.	.	.	.	.	.
Thymus serpyllum	.	I	III	II	r	IV	V	II	I	+	.	.	.	.	r	.
Rumex acetosella	I	II	II	I	II	III	II	III	.	I	.	.	.	.	.	.
Danthonia decumbens	I	I	III	III	III	II	I	II	+	+	.	.	.	.	.	.
Campanula rotundifolia	IV	II	II	II	IV	+	r	II	+	r	.	.	.	.	.	.
Peucedanum oreoselinum	I	r	r	IV	III	V	V	IV	III	IV	.	.	.	.	.	.
Deschampsia flexuosa	III	V	V	IV	III	III	r	+	I	+	.	.	.	.	.	.
Veronica officinalis	IV	II	IV	II	IV	III	III	III	II	II	.	.	.	.	.	.
Dicranum scoparium	II	I	I	II	+	III	II	II	I	II	.	.	.	.	.	.
Convallaria majalis	+	.	I	+	I	V	V	III	V	IV	.	.	.	.	.	.
Polytrichum formosum	II	I	I	I	II	.	+	r	I	II	.	.	.	.	.	.
Luzula campestris	.	II	II	II	II	II	+	II	+	+	.	.	.	.	.	.
Moneses uniflora	+	I	II	+	r	.	.	r	r	r	.	.	.	.	.	.
Anthericum ramosum	.	r	r	.	III	III	II	II	II	II	.	.	.	.	.	.
Monotropa hypopitys	.	r	r	I	.	+	I	II	I	II	.	.	.	.	.	.
Polytrichum juniperinum	.	r	r	II	.	II	III	II	I	I	.	.	.	.	.	.
Scorzonera humilis	.	.	+	+	.	V	V	III	IV	IV	.	.	.	.	.	.
Cytisus nigricans	.	.	.	+	.	II	.	II	.	r	.	.	.	.	.	.
Lycopodium clavatum	.	.	.	r	.	+	+	I	I	I	I	II	III	.	.	.
Diphasiastrum complanatum	.	.	.	.	.	II	III	+	I	+	I	II	II	.	.	.
Hypochaeris maculata	.	.	.	.	.	r	I	r	r	.	.	I	II	.	r	.
Trientalis europaea	.	.	.	.	.	II	II	III	IV	V	.	.	IV	.	.	.
Galium boreale	.	.	.	r	.	.	.	.	.	.	I	I	III	IV	II	V
Lathyrus vernus	.	.	.	.	.	.	.	.	.	.	I	I	III	I	I	II
Lupinaster pentaphyllus	.	.	.	.	.	.	.	.	.	.	V	V	V	I	IV	IV
Dianthus versicolor	.	.	.	.	.	.	.	.	.	.	III	III	.	.	I	.
Rubus fruticosus agg.	IV	II	III	+	II	.	.	.	.	.	.	.	.	.	.	.
Hieracium sylvaticum	III	II	+	III	III	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum	II	III	III	.	II	.	.	.	.	.	.	.	.	.	.	.
Carex pilulifera	.	III	II	+	III	.	.	.	.	.	.	.	.	.	.	.
Euphorbia cyparissias	IV	I	I	II	III	.	.	.	.	.	.	.	.	.	.	.
Brachypodium sylvaticum	V	II	II	+	II	.	.	.	.	.	.	.	.	.	.	.
Rubus idaeus	I	III	II	+	+	.	.	.	.	.	.	.	.	.	.	.
Mycelis muralis	III	III	I	+	r	.	.	.	.	.	.	.	.	.	.	.
Asparagus officinalis	II	+	+	r	II	.	.	.	.	.	.	.	.	.	.	.
Moehringia trinervia	III	I	I	r	I	.	.	.	.	.	.	.	.	.	.	.
Hypochaeris radicata	.	I	I	II	r	.	.	r	.	r	.	.	.	.	.	.
Dianthus carthusianorum	I	r	.	I	II	+	.	+	.	.	.	.	.	.	.	.
Scabiosa canescens	II	.	.	.	II	.	.	.	.	.	.	.	.	.	.	.
Pulsatilla verna	.	.	.	II	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sanguineum	+	.	.	.	.	I	II	I	I	II	.	.	.	.	.	.
Cytisus ruthenicus	.	.	.	.	.	.	r	I	+	II	.	.	.	.	.	.
Oxalis acetosella	.	.	.	.	.	.	r	+	r	IV	.	.	.	.	.	.
Arctostaphylos uva-ursi	.	.	.	.	.	IV	IV	+	I	r	.	.	.	.	.	.
Pulsatilla pratensis	.	.	.	.	r	II	r	r	.	.	.	.	.	.	.	.
Lycopodium annotinum	.	.	.	r	.	+	+	+	r	II	.	.	.	.	.	.
Veronica spicata	.	r	.	.	.	.	.	.	.	.	IV	II	I	.	.	.
Vicia sepium	.	.	.	.	.	.	.	.	.	.	II	III	IV	.	.	.
Eremogone saxatilis	.	.	.	.	.	.	.	.	.	.	III	I	.	.	.	.
Carex supina	.	.	.	.	r	.	.	.	.	.	IV	III	.	.	.	.
Cnidium dubium	.	.	.	.	.	.	.	.	.	.	I	.	V	.	.	.
Fragaria viridis	.	.	.	.	r	.	.	.	.	.	.	I	IV	.	.	.

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