

## Soil-moisture conditions indicated by field-layer plants help identify vulnerable forests in the forest-steppe of semi-arid Southern Siberia



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### ABSTRACT

High variability in soil-moisture conditions is typical for semi-arid forest-steppe ecosystems where precipitation varies greatly over time. Plant species that inhabit these environments integrate responses to broadly fluctuating wetness conditions. Indirect assessment of contrasting habitat wetness based on plant indicator values, species frequency, and species coverage was carried out in two sites representing the larch (*Larix sibirica*) and pine (*Pinus sylvestris*) forest-steppe communities. For the larch forest-steppe, we found that plant community composition and spatial structure depended strongly on wetness. In addition, we found that the vegetation was clearly differentiated into forest stands and steppe communities, depending on the slope aspect. There was also a strong correlation between dissimilarities of species composition and differences in habitat wetness revealed in the larch forest-steppe. In contrast, soil properties, such as gravel and stone content were found to be a key factor in the spatial distribution of plant species composition in the pine-forest-steppe communities. Indirect assessment of moisture conditions in the forest-steppe habitats, based on the field-layer plant species, was found to be preferable for indicating soil water deficits in the forest. Furthermore, as long-term observational data is often lacking, indirect assessment of the forest-steppe vegetation provides an opportunity to identify vulnerable forests at the marginal distribution. Based on indirect assessments of soil-moisture conditions, and taking into account differences in potential drought resistance between larch and pine forests, we concluded that increasing aridity will cause the replacement of Siberian larch by Scots pine in the South Siberian forest-steppe landscape. Consequently, in the future it is likely that forest-steppe typological diversity will decrease, and the semi-arid landscape may become more monotonous.

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### 1. Introduction

High variability in soil-moisture conditions, depending on weather fluctuations, is a well-known phenomenon. Significant variability is typical for semi-arid ecosystems where precipitation varies greatly in spatial and temporal distribution in comparison with humid and arid territories. For this reason, determining wetness gradients requires long-term monitoring studies and specific

analytical methods. Synoptic data from precipitation gauges can provide a general overview of soil-moisture differentiation among various ecosystems. These assessments provide information of a coarse and relative nature, but are often insufficient for determining vegetation community patterns, in addition to forests suffering from water deficit.

An integrated response to broadly fluctuating wetness conditions can be deduced from the plant species inhabiting such environments (Zonneveld, 1983; Diekmann, 2003). In the early 1950s, German ecologist Heinz Ellenberg and Russian geobotanist Leontyi G. Ramensky independently developed indicator systems for vascular plants. The first edition of the indicator values, developed by Ramensky et al. (1956), covered the European portion of the former USSR. The name given by the author for this indicator system was "standard ecological scale". L.N. Sobolev and V.D.

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Utekhin (1982), along with R.P. McIntosh (1983) described Ramensky's approach in English.

As the data on plant ecology and geography were extended, vegetation of other regions was included in the “standard ecological scale”. These areas included Siberia (Tsatsenkin et al., 1974, 1978; Korolyuk, 2006) and the Russian Far East (Komarova et al., 2003). Ellenberg (1974) published a list of indicator values for vascular plants occurring in central Europe based on preliminary studies from the early 1950s. The latest edition was sufficiently expanded and included values for bryophytes and lichens (Ellenberg et al., 1991). There is also a well known alternative list of indicator values proposed for Switzerland (Landolt, 1977; Landolt et al., 2010). Although researchers independently developed plant indicator values, in general, the approaches were quite similar.

The indirect assessment method and characterization of habitat wetness based on indicator values of plants combine intensive long-term procedures and single measurements. Plant species composition reflects the wetness conditions to which the communities are exposed over time, and therefore, plant communities can integrate a longer time period through the later application of plant and community indicator values. Evaluation of the plant indicator values and weighted averages has been found to be possible for the indirect assessment of long-term community exposure patterns. For example, several researchers have found correlations between assessments based on indicator values and direct environmental traits measurement (e.g., Diekmann, 1995; Diekmann and Dupre, 1997; Diekmann and Falkengren-Grerup, 1998; Ertsen et al., 1998; Dzwonko, 2001). In addition, Kopecký and Čížková (2010) reported that the Topographic Wetness Index (TWI), computed from an analysis of the contributing upslope area, was correlated with habitat wetness estimates based on Ellenberg's (1974) indicator values. Thereafter, Moeslund et al. (2013) found a correlation between TWI and the Ellenberg indicator values (moisture) calculated for relevés in lowland region (in Denmark). Thus, there is evidence that plants integrate conditions to which they are exposed over time, and assessments based on the indicator value of plants might be acceptable for the evaluation and characterization of soil-moisture conditions. Compared to direct measuring with a gauge, such assessments are also more ecologically relevant because reflect plant organism's general responses to environmental conditions.

In southeastern Siberia increasing climate aridity originates from a combination of significant climate warming (Mokhov et al., 2006) and relatively stable humidity in the region (Gruza et al., 2007; Sirotenko et al., 2007). The locally estimated warming trend was reported to be 0.05–0.08 °C per year (Kulikov et al., 2009), and demonstrated accelerated warming during the second half of the 20th century (Ippolitov et al., 2007).

Forests are water-deprived next to the water limit just within the forest-steppe ecotone. In the southern part of the lake Baikal region where the forest-steppe landscapes are predominant, the increasing aridity has become especially apparent (Smirnova, 2004; Ubugunov and Kulikov, 2013). These landscapes are defined by the sharp contrast of insolation intensity between the northern and southern slopes, which result in strong differences in the temperature and available moisture, as was already discussed (Bennie et al., 2008; Burnett et al., 2008; Liu et al., 2013; Moeslund et al., 2013). At the same time, forest-steppe communities are responsive to aridization (Allen and Breshears, 2007; Frelich and Reich, 2009; Bailey, 2011) because forests are critically dependent on wetness. Prolonged water deficits stipulate extensive tree die-offs (Fensham et al., 2009).

Forests have globally and regionally suffered from drought and heat events, together with increasing climate aridity (e.g. Allen et al., 2010; Kharuk et al., 2013; Liu et al., 2013). The use of vulnerability assessments in forest communities is a significant

topic, as climate warming and drought-caused alterations in the composition of forest species can drive vegetation-type conversions, promote new plant-community assemblages, resetting or shifting successional trajectories (Anderegg et al., 2013). Besides, semi-arid forests have global importance because of substantial carbon sequestration and subsequent cooling effects (Rotenberg and Yakir, 2010). At the same time, forests are critically important for environmental monitoring in semi-arid regions, which support approximately 36% of the world's human population and highly diverse flora and fauna (Millennium Ecosystem Assessment, 2005; Carpenter et al., 2009). There are, however, no observational studies addressing the effects of changes in habitat wetness on the community diversity and structure within the forest-steppe ecosystems. Moreover, there is a lack of data necessary to assess current wetness conditions and probable future habitat deterioration under increasing aridity.

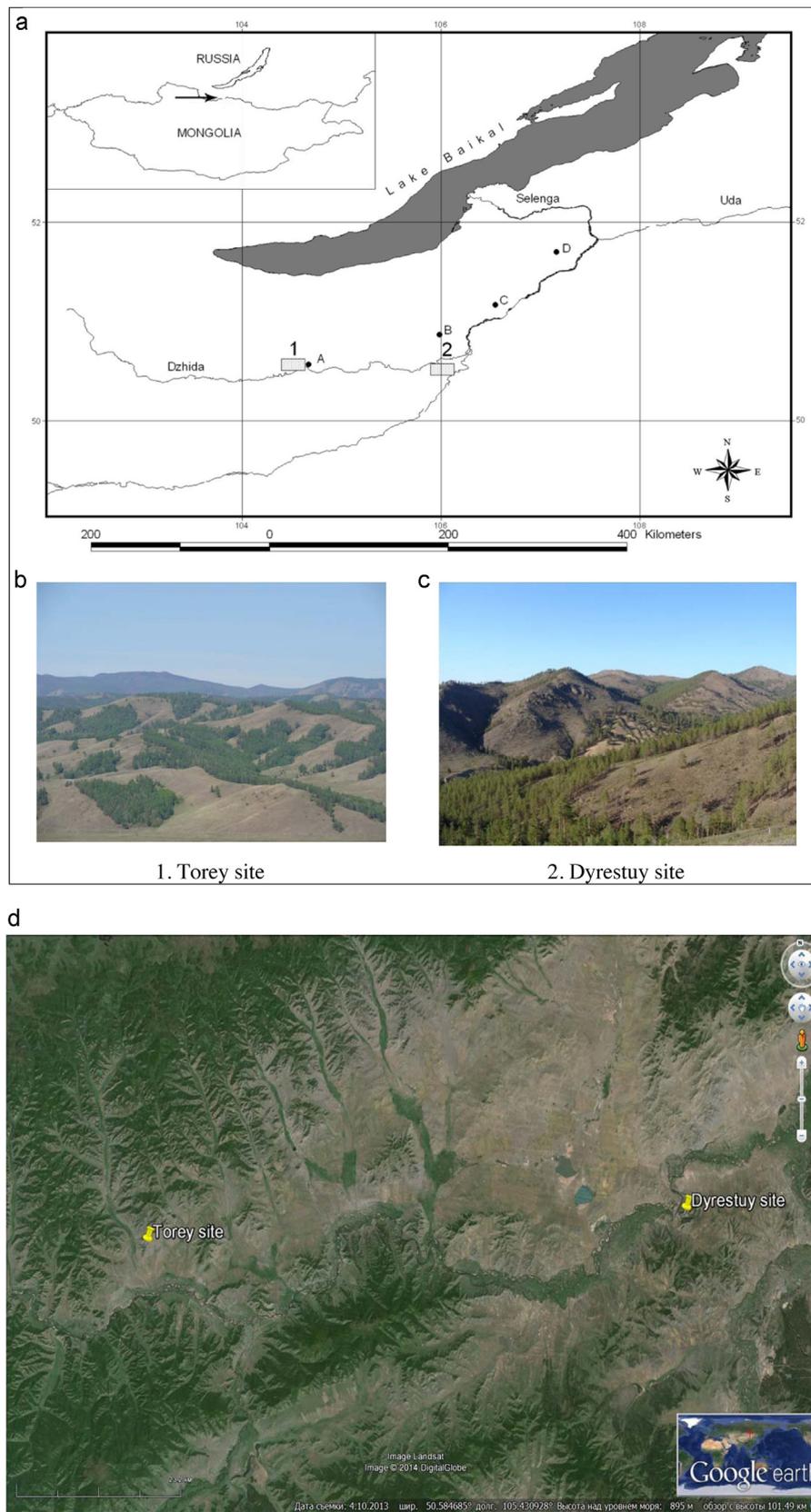
Due to some tree species succumbing more readily than others (e.g. Mueller et al., 2005), reliable approaches to exploring the resilience of different tree species to habitat moisture shortage are needed. It remains unclear what kind of forest stands are the most vulnerable under a decreasing soil water supply and increasing climate aridity. This presents a barrier to predictions on probable climate-forced vegetation dynamics and/or transformations of forest-steppe ecosystems. Thus, we hypothesized that wetness condition indicated by ground plant species determines forest distribution in the forest-steppe ecotone and it is possible to identify the forest patches facing the greatest water deficit. To enable a better understanding of how Siberian forest-steppe communities depend on soil moisture dynamics and to pave the road for a better protection of these ecosystems during future climate changes we investigated the following: (1) does the wetness condition indicated by understory plant species determine forest distribution in the forest-steppe ecotone? (2) If yes, is it possible to use this information to identify the forest patches facing the greatest water deficit?

## 2. Materials and methods

### 2.1. Study sites

The study area was located to the south of Lake Baikal (50°29'–50°30' N, 104°37'–105°58' E) and covered about 950 km<sup>2</sup> of the Dzhida River valley in the foothills of the Khमार-Daban and Dzhidinskiy mountain ridges (Fig. 1). The elevation ranged from 650 m a.s.l. at the valley's bottom to 1100 m a.s.l. The study area was in the semi-arid region of the middle temperate physiographic zone, and the larch (*Larix sibirica* Ledeb.) and Scots pine (*Pinus sylvestris* L.) forest-steppe vegetation are predominant in the area (Vipper, 1968). Elm (*Ulmus pumila* L.) and steppe-shrub communities also occupied some patches. In general, the typical pattern of the forest-steppe (Lavrenko et al., 1991), characterized by physiognomic contrast, occurred. Namely, forest patches occupy northern slopes, and steppe vegetation grows on the southern slopes. Eastern and western slopes are covered by steppe, but sometimes forest patches in locally more humid conditions are also found there.

The coniferous forests belong to the hemiboreal Asian class *Rhytidio-Laricetea* K. Korotkov et Ermakov 1999 (Ermakov, 2003), while the steppe communities belong to the class *Cleistogenetea squarrosae* Mirkin et al., 1986 of Eastern Siberia and Central Asia (Hilbig, 1995; Gadghiev et al., 2002). Geographically, the forest-steppe vegetation represents the transitional zone between the East Siberian taiga and the Mongolian steppes. Historically, the larch and pine forests have dominated the regional vegetation over the last 3000 years, a period characterized by decreased humidity and a more continental climate (Tarasov et al., 2002).



**Fig. 1.** Study area location. Study sites are indicated by numbered rectangles; Torey (1) and Dyrestuy (2). Black dots show localities of larch and pine woodlands where the soil-moisture content has been measured: A – larch woodland near Torey (50.566424 N 104.667640 E); B – pine woodland near Dyrestuy (50.864890 N 105.985927 E); C – pine woodland near Dyrestuy (51.167332 N 106.545947 E); D – pine woodland at the eastern part of the Khamar-Daban mountain ridge (51.70033 N 107.16358 E).

Two sites within the area were studied: Dyrestuy (eastern site), and Torey (western site; see Fig. 1). The general climatic features of the study area were defined as being continental with a high level of variability in the annual and diurnal air temperatures. The sites were distributed along a gradient of mean annual precipitation (MAP), ranging from 200 mm to 310 mm, but with a similar mean annual temperature of around  $-2^{\circ}\text{C}$  ([www.worldclim.org](http://www.worldclim.org)). Along this gradient, the grassy larch forests replaced the dry pine forests with sparse plants in the ground layer. In addition, the bunch-grass steppe communities formed by xerophytes transitioned to the meadow-grass steppe. The soils of the Torey site were characterized as leached chernozems and gray forest soils, while the Dyrestuy site soils were characterized as chestnut soils (Nogina, 1964). Importantly, the soils in the pine woodlands at the Dyrestuy site were often primitive with typical textures of mostly sand, gravel, or stone.

## 2.2. Analysis of vegetation pattern

A total of 340 relevés (100 m<sup>2</sup> each, mostly 10 m × 10 m) were sampled for the vegetation analysis: 115 at Torey and 225 at Dyrestuy. We avoided areas with significant gypsy moth (*Lymantria dispar asiatica* Vunkovskij) damage, so vegetation could be considered as being relatively undisturbed. Relevés at each site were plotted along different hillsides, taking into account slope and aspect, ranging from 0° to 359°, as measured by a compass (see Table 1). Because aspect is a circular variable, it was transformed into “southness” (Chang et al., 2006):

$$S = 180 - |\text{Expo} - 180|$$

where *Expo* – aspect (slope exposition in degrees).

The plant species within each plot were identified, and the cover (%) for each species was visually evaluated. In total, 351 plant species were identified and counted, following the Cherepanov's (1995) nomenclature. IBIS 6.2 software (Zverev, 2007; see Appendix 1) was used for vegetation data storage and analysis.

The ecological features of the vegetation data set were analyzed using both single relevés and synthetic relevés. The synthetic relevé was created in IBIS 6.2, and was comprised of species from relevés found in similar sites, as identified by aspect and slope. A combination of relative frequency (%) and cover as the most common variables was widely used in vegetation science (Cottam and Curtis,

1956; Wang et al., 2002; Jolley et al., 2010). This combination, called the Importance Value represented the universal index for the analyses of the patterns in plant communities. The relative frequency (*RF*) and mean cover (*MC*) for every species (*i*) were computed. Then, the importance values (*P*) for each species in plant communities were calculated:

$$P(i) = \sqrt{RF(i) * MC(i)}$$

Sørensen's coefficient (*SC*; Sørensen, 1948) was used to calculate similarity between relevés, while Bray–Curtis's coefficient (*BCC*; Bray and Curtis, 1957) was used to compare between synthetic relevés. The *BCC* takes into account species relative frequency within the set of relevés.

Because relevés were collected along all ranges of the slope and aspect variables, the relative frequency rate reflected the actual plant species distributions throughout different plant communities. Hence, the *BCC* combined both the individual and phytocoenotic significance of a given species in a landscape. A low value of this index reflects high levels of contrast between the northern and southern slopes.

To find the most contrasting differences in the species composition between the aspect variables, the sets of relevés from the Torey and Dyrestuy sites were divided into eight groups, according to aspect, in classes of 45° (Table 1). The similarity/dissimilarity between the relevés was computed, and then compared according to these eight groups. As a result, the maximal dissimilarity between the groups from the northern (315–45°) and southern (135–225°) sectors was revealed. On this basis, two subsets of relevés from both sites, representing the northern and southern sectors, were selected for further processing. In total, 109 relevés were selected: 33 from southern slopes and 23 from northern slopes in Torey, in addition to the 21 southern and 32 northern relevés in Dyrestuy. From these four relevé groups, we developed an additional four synthetic relevés and calculated the *SC* between the groups.

## 2.3. Assessment of habitat wetness using plant species indicator values

We used the Student's *t*-test to estimate soil wetness differences between the southern and northern slopes. Using plant species indicator values for southern Siberia (Tsatsenkin et al., 1974, 1978; Korolyuk, 2006), the Indicator Value for Moisture (*IVM*) for every

**Table 1**  
Distribution of relevés according to slope and aspect in Torey and Dyrestuy.

Inclination	Aspect, degrees					Total
	Plane	North (316–45)	East (46–135)	South (136–225)	West (226–315)	
Number of relevés, Torey						
0°	6					6
1–4°		3	4	4	3	14
5–9°		1	5	6	3	15
10–14°		5	4	8	5	22
15–19°		8	5	4	5	22
20–24°		3	4	5	4	16
>24°		3	3	6	8	20
Total	6	23	25	33	28	115
Number of relevés, Dyrestuy						
0°	40					40
1–4°		11	4	7	14	36
5–9°		8	4	1	12	25
10–14°		17	7	8	15	47
15–19°		3	3	5	7	18
20–24°		4	1	2	10	17
>24°		7	10	12	13	42
Total	40	50	29	35	71	225

**Table 2**  
Sørensen's coefficient averages between plant communities grouped according to the slope aspect at the Torey site.

Slope sectors Degrees	N	E		S		W		N
	1–45	46–90	91–135	136–180	181–225	226–270	271–315	316–360
0–44	0.40	0.25	0.17	0.14	0.15	0.15	0.22	0.36
45–89		0.38	0.31	0.27	0.30	0.31	0.35	0.22
90–134			0.46	0.36	0.38	0.39	0.39	0.15
135–179				0.38	0.39	0.37	0.35	0.11
180–224					0.48	0.43	0.42	0.10
225–269						0.46	0.41	0.12
270–314							0.48	0.18
315–359								0.42

relevé was calculated. The indicator value represented the optimal position of a species along a wetness gradient, ranging from 1 (absolutely dry) to 120 (aquatic habitats). The plant community *IVMs* of the studied sites ranged from 45 to 60, corresponding to the typical bunch-grass steppe and mesophytic grassy woodlands respectively (Korolyuk, 2008). The most xerophytic plant (*Enneapogon borealis* (Griseb.) Honda) had an indicator value of 26, and the most hygrophytic (*Pedicularis resupinata* L.) had an *IVM* of 72. The *IVM* was calculated as the average of the total importance values of all species registered within the plot. To calculate the matrix-based correlation between the *SC* and *IVM* differences, we used Mantel's test ( $R_m$ ), with 10,000 permutations (Mantel, 1967), integrated into the PAST 2.17 software (Hammer et al., 2001). This correlation showed the relationships between *SC* and habitat wetness, as measured by *IVM*. To visualize the results obtained, we used the "hill modeling" approach (Korolyuk, 2008; see also Appendix 2).

#### 2.4. Test of model assessment with field measurements

Unlike parameters of habitat wetness received by plant species indicator values, the results of single humidity measurements were highly volatile. In order to test the volatility of the air's humidity (which is connected with the highly variable air temperature) defined over the course of short observations, the measurements were taken using gauges. The humidity and temperature at the grass level (approximately 2 cm from the top of the soil), as well as soil temperature, were obtained using an Oakton Digital Thermohygrometer and Bi-Metal Dial Thermometer. Measurements were taken only once, at the time, in the beginning of August. Measurements were taken during one sunny day for one hour after midday with at least five replications at each point. The mean values of the replications were used for further analysis. In total, 30 points representing different slopes and orientations were measured at Dyrestuy site.

Soil moisture was determined in larch and pine forests within the study sites in plots, measured at the same time for all relevés. The samples were taken once during similar weather conditions for all of the sampling areas. In each stand, soil samples were taken from three randomly chosen plots on the northern and southern slopes. The soil was sampled in three replications every 10 cm down to 50 cm in depth. The samples were weighed then oven dried at 105 °C for 24 h. Soil moisture was calculated as the difference between the wet and dry weights (the mean of three replications).

Distributions of variables were checked for normality using Kolmogorov–Smirnov, Lilliefors, and Shapiro–Wilk's tests. We found all of variables, excepting air humidity ( $p < 0.10$ ,  $p < 0.01$ ,  $p = 0.00671$ , for abovementioned tests respectively), were significantly compliant with normal distribution. Thereafter the interrelation between directly measured air humidity and *IVM*, as well as between *IVM* and the results of the soil moisture field measurements was statistically tested. In order to keep the statistical safety, both Pearson's linear correlation

coefficient ( $r$ ) and Spearman's rank correlation coefficient ( $r_s$ ) were calculated.

### 3. Results

#### 3.1. Species composition similarities and community similarities of the two sites

The results of the *SC* similarity between the eight groups (see Section 2.2) are shown in Table 2. The most significant dissimilarities were found between the northern slopes and all of the other slopes. The species composition at the southern and northern slopes sites in Torey and Dyrestuy was similar (*SC* values of 0.53 and 0.58 respectively). Consequently, the level of difference in species composition at the habitats located on opposite slopes was almost equal at the both sites.

According to the *BCC* calculations, substantial dissimilarities between the synthetic relevés at the southern and northern slopes in Torey and Dyrestuy were found, with *BCC* values of 0.32 and 0.47, respectively. Despite the level of differences in species composition being almost similar at both sites, the synthetic relevés *BCC* comparison showed a considerably higher level of contrast at Torey compared to Dyrestuy. When including the importance values ( $P$ ) into the *BCC* calculations, contrasts between the opposite slope communities were yielded, with these results being higher than the combined *BCC* index: 0.23 in Torey, and 0.43 in Dyrestuy.

There were many plant species that preferred to grow on the northern (covered by forest) or southern slopes (covered by steppe) at the Torey site: 28 sylvan and 32 steppe inhabitants, respectively (see Table 3). Among sylvan differentials, mesophytic and xeromesophytic plants prevailed, but five species were frequently found growing in the stony or gravelly steppe communities. The differential group of species on the southern slope was comprised of steppe plants that inhabited well-developed and primitive stony and gravelly soils. The group of joint species was composed of 17 primarily meadow-steppe plants, in addition to several plants having wide ecological amplitudes within the wetness factor ranges. In general, differential groups of plant species reflected presence of differences between conditions that were conducive to the development of steppe communities on the southern slopes and dense forests on the northern slopes.

In comparison to the Torey site, the group of differential species at the Dyrestuy site was less numerous than was the group of joint species (Table 3): 17 species in the northern-facing slope group and seven species in the southern-facing slope group. A total of 41 species were recorded on both slopes. Xerophytic steppe plants were represented in all groups. Although the species contrast (as measured by *SC* similarities) between the northern and southern slopes was quite similar at both sites, plant communities at the Torey site had a sufficiently greater level of contrast when compared to Dyrestuy.

A bimodal pattern for the distribution of the species frequency differences between opposite slopes at the Torey site was revealed

**Table 3**  
Frequency (PO, %) and mean coverage (MC, %; indicated when it is over 1%) of the plant species at the Torey and Dyrestuy sites.

Torey			Dyrestuy		
Species	Northern slope PO (MC)	Southern slope PO (MC)	Species	Northern slope PO (MC)	Southern slope PO (MC)
<b>Differential species for northern slopes</b>			<b>Differential species for northern slopes</b>		
<b>Trees and shrubs</b>			<b>Shrub</b>		
<i>Larix sibirica</i>	90 (36)	.	<i>Caragana pygmaea</i>	56 (1)	14
<i>Betula platyphylla</i>	48 (7)	.	<b>Ground layer</b>		
<i>Cotoneaster melanocarpus</i>	81 (2)	3	<i>Veronica incana</i>	63 (3)	5 (1)
<i>Spiraea media</i>	57 (5)	3	<i>Saussurea salicifolia</i>	59	5
<i>Rosa acicularis</i>	38 (1)	.	<i>Poa botryoides</i>	56	5
<b>Ground layer</b>			<i>Artemisia frigida</i>	72 (3)	24
<i>Sanguisorba officinalis</i>	95 (1)	3	<i>Dianthus versicolor</i>	56	10
<i>Fragaria orientalis</i>	90 (8)	.	<i>Aster alpinus</i>	44	
<i>Artemisia tanacetifolia</i>	90 (6)	3	<i>Carex pediformis</i>	72 (3)	29 (1)
<i>Dendranthema zawadskii</i>	86 (7)	3	<i>Scabiosa comosa</i>	47	5
<i>Rhynchidium rugosum</i>	81 (24)	.	<i>Oxytropis turczaninovii</i>	41	
<i>Lathyrus humilis</i>	76 (6)	.	<i>Astragalus suffruticosus</i>	41	
<i>Festuca ovina</i>	81 (3)	9 (1)	<i>Eremogone meyeri</i>	38	
<i>Iris ruthenica</i>	71 (5)	.	<i>Potentilla acaulis</i>	41 (2)	5
<i>Pulsatilla patens</i>	71 (4)	.	<i>Heteropappus altaicus</i>	41	5
<i>Lupinaster pentaphyllus</i>	67 (1)	.	<i>Koeleria cristata</i>	72 (2)	38 (1)
<i>Thalictrum foetidum</i>	71 (2)	6	<i>Festuca sibirica</i>	38 (1)	5
<i>Sedum aizoon</i>	67	3	<i>Schizonepeta multifida</i>	47	14
<i>Artemisia sericea</i>	62 (4)		<i>Aconogonon angustifolium</i>	31	
<i>Scorzonera radiata</i>	62 (1)		<i>Erysimum flavum</i>	31	
<i>Aster alpinus</i>	86 (3)	24 (1)	<b>Differential species for southern slopes</b>		
<i>Astragalus inopinatus</i>	48		<b>Tree</b>		
<i>Carex macroura</i>	48 (3)		<i>Ulmus pumila</i>	6	62 (1)
<i>Vicia unijuga</i>	48 (2)		<b>Ground layer</b>		
<i>Vicia nervata</i>	48 (1)	3	<i>Lespedeza davurica</i>		62
<i>Carex pediformis</i>	62 (6)	18	<i>Lespedeza juncea</i>	6	62
<i>Elymus gmelinii</i>	48 (1)	9	<i>Stellaria dichotoma</i>	34 (1)	71 (1)
<i>Aconitum barbatum</i>	38 (1)		<i>Potentilla tanacetifolia</i>	13	48
<i>Pedicularis rubens</i>	38		<i>Chamaerhodos erecta</i>	19	52
<b>Differential species for southern slopes</b>			<i>Patrinia rupestris</i>	16	48
<b>Ground layer</b>			<b>Joint species</b>		
<i>Cleistogenes squarrosa</i>		73 (2)	<b>Shrubs</b>		
<i>Lespedeza juncea</i>		70 (4)	<i>Spiraea aquilegifolia</i>	34 (1)	48 (1)
<i>Aconogonon angustifolium</i>	10	79	<i>Rhamnus erythroxylon</i>	6	24 (1)
<i>Dontostemon integrifolius</i>	5	73 (2)	<b>Ground layer</b>		
<i>Eremogone meyeri</i>	5	73 (1)	<i>Pulsatilla turczaninovii</i>	78 (1)	57 (1)
<i>Lilium pumilum</i>	10	76 (1)	<i>Polygala tenuifolia</i>	59	71
<i>Agropyron cristatum</i>		61 (3)	<i>Achnatherum sibiricum</i>	66 (1)	57 (1)
<i>Thymus baicalensis</i>		61 (4)	<i>Artemisia gmelinii</i>	44 (1)	71 (4)
<i>Polygala tenuifolia</i>	5	64 (1)	<i>Stemmacantha uniflora</i>	59	48
<i>Artemisia frigida</i>		58 (2)	<i>Lilium pumilum</i>	47	52
<i>Chamaerhodos erecta</i>		58 (1)	<i>Artemisia commutata</i>	53	33
<i>Potentilla sericea</i>	5	58	<i>Filifolium sibiricum</i>	56 (1)	29 (2)
<i>Potentilla acaulis</i>		48	<i>Cleistogenes squarrosa</i>	44	38
<i>Allium tenuissimum</i>		48 (6)	<i>Carex korshinskyi</i>	41 (1)	38 (1)
<i>Pulsatilla turczaninovii</i>	29	73 (4)	<i>Cymbaria daurica</i>	34	38 (1)
<i>Poa botryoides</i>	33 (1)	76 (3)	<i>Galium ruthenicum</i>	44	24
<i>Carex argunensis</i>		42 (3)	<i>Youngia tenuifolia</i>	38	24
<i>Silene aprica</i>		42	<i>Potentilla longifolia</i>	25	33
<i>Stellaria cherleriae</i>		42	<i>Scorzonera austriaca</i>	28	29
<i>Amblynotus rupestris</i>	5	45	<i>Bupleurum scorzonerifolium</i>	38	19
<i>Alyssum obovatum</i>		39	<i>Goniolimon speciosum</i>	34	19
<i>Carex duriuscula</i>		39 (1)	<i>Saposhnikovia divaricata</i>	28	24
<i>Orostachys spinosa</i>		39 (2)	<i>Sedum aizoon</i>	22	29
<i>Leibnitzia anandria</i>	10	48 (1)	<i>Orostachys spinosa</i>	34 (1)	14
<i>Festuca lenensis</i>	5	42 (4)	<i>Stipa baicalensis</i>	34 (1)	14
<i>Artemisia scoparia</i>		36 (1)	<i>Cleistogenes kitagawae</i>	9	38 (1)
<i>Filifolium sibiricum</i>	5	39 (3)	<i>Rubia cordifolia</i>	13	33
<i>Stemmacantha uniflora</i>		33	<i>Polygonatum sibiricum</i>	9	33 (1)
<i>Potentilla bifurca</i>	10	42 (1)	<i>Selaginella sanguinolenta</i>	28 (4)	14 (1)
<i>Achnatherum sibiricum</i>	19 (1)	52 (3)	<i>Serratula centauroides</i>	28	14
<i>Stellera chamaejasme</i>	24	55 (1)	<i>Galium verum</i>	13	29
<i>Arctogeron gramineum</i>		30 (1)	<i>Thymus baicalensis</i>	25	14
<b>Joint species</b>			<i>Alyssum lenense</i>	13	24
<b>Ground layer</b>			<i>Stellaria cherleriae</i>	31	5
<i>Potentilla longifolia</i>	48 (2)	67 (1)	<i>Allium tenuissimum</i>	28	5
<i>Koeleria cristata</i>	43 (1)	67 (2)	<i>Agropyron cristatum</i>	3	29
<i>Bupleurum scorzonerifolium</i>	57 (1)	52 (1)	<i>Carex argunensis</i>	3	29 (3)
<i>Youngia tenuifolia</i>	57	48	<i>Alyssum obovatum</i>	22	10
<i>Patrinia rupestris</i>	38	36	<i>Allium bidentatum</i>	22	10

Table 3 (Continued)

Torey			Dyrestuy		
Species	Northern slope PO (MC)	Southern slope PO (MC)	Species	Northern slope PO (MC)	Southern slope PO (MC)
<i>Galium verum</i>	48 (1)	18 (1)	<i>Asparagus burjaticus</i>	6	24
<i>Schizonepeta multifida</i>	33 (1)	21	<i>Allium anisopodium</i>	16	14
<i>Scabiosa comosa</i>	24	27 (2)	<i>Potentilla verticillaris</i>	25	5
<i>Allium strictum</i>	33	12	<i>Festuca lenensis</i>	25 (1)	5
<i>Artemisia gmelinii</i>	19	21 (3)			
<i>Dianthus versicolor</i>	5	33			
<i>Kitagawia baicalensis</i>	14	21			
<i>Cymbaria daurica</i>	5	30 (1)			
<i>Serratula centauroides</i>	5	30			
<i>Artemisia commutata</i>	10	24 (1)			
<i>Carex korshinskyi</i>	5	27 (2)			
<i>Scutellaria scordiifolia</i>	19	12			

(Fig. 2). The reason for this was that there were many plant species strictly confined to slopes oriented to the north or south. Those species formed two peaks on the histogram (Fig. 2, left) representing cores of differential groups. At the Dyrestuy site, the inverse situation occurred: the group comprised of species that had no obvious preference was considerably larger than was the differential one, resulting in a unimodal distribution pattern (Fig. 2) that did not appear to be particularly affected by the slope orientation. The latter is resulted in a high similarity between plant species composition on the northern and southern slopes at the Dyrestuy site.

### 3.2. Pattern of plant life forms distribution

Clear discrepancies among the life form distribution along the slopes of the contrasting orientation were observed at the Torey site. Three shrub species (*Cotoneaster melanocarpus* Fisch. ex Loudon, *Spiraea media* Fr. Schmidt, *Rosa acicularis* Lindl.) usually formed the understorey and were confined to the northern slopes. At the ground layer, the moss species *Rhytidium rugosum* (Hedw.) Kindb. was associated with the northern slopes. Herbaceous perennial and annual plants, as well as xerophytic dwarf subshrubs, represented the southern slopes group. Trees, shrubs, and mosses were much less important in plant communities on the southern slopes (see Table 3). Trees, such as larch (*L. sibirica*) and birch (*Betula platyphylla* Sukaczev), were strictly confined to the northern slopes with a high frequency, specificity, and abundance. Larch was the main dominant species (mean coverage is 36%), and birch trees were normally admixtures (mean coverage

is 10–15%). Birch is well-known as a secondary tree and tends to be dominant in post-disturbed areas (e.g., after burning and gypsy moth infestations). Recent studies showed that gypsy moth attacks might have been the cause of spatial shifts at the forest-steppe borderline by increasing the mortality of mature trees and inhibiting rejuvenation (Hauck et al., 2008). However, no sufficient burning or insect infestations have happened over the past few decades. Thus, the vegetation in the study site was relatively undisturbed and the abovementioned life form distribution pattern represented the natural situation in the region.

### 3.3. Assessment of soil moisture patterns of the two sites

According to the IVM analysis, the mean difference of wetness between the northern and southern slopes at the Torey site was significant according to the Student's *t*-test ( $p < 0.0010$ ; Table 4). The average wetness for the northern slopes at the Torey site was 57 levels. For the whole area of southern Siberia, this ranking is accorded to the transitional belt between the steppe meadow on one side, and the grassy forest and typical meadow on the other side. The average wetness for the southern slopes was 50 levels, which is accorded to the species-rich bunch-grass steppe. The significance of the seven-level wetness interval between the opposite slopes was notable as it was located along an important border differentiating steppe and meadow vegetation. The range of 50–57 levels characterizes the habitats of the meadow-steppe communities. Differences in the IVM between the slopes at the Dyrestuy site were less than one level, and were not statistically different ( $p = 0.2218$ ; Table 4).

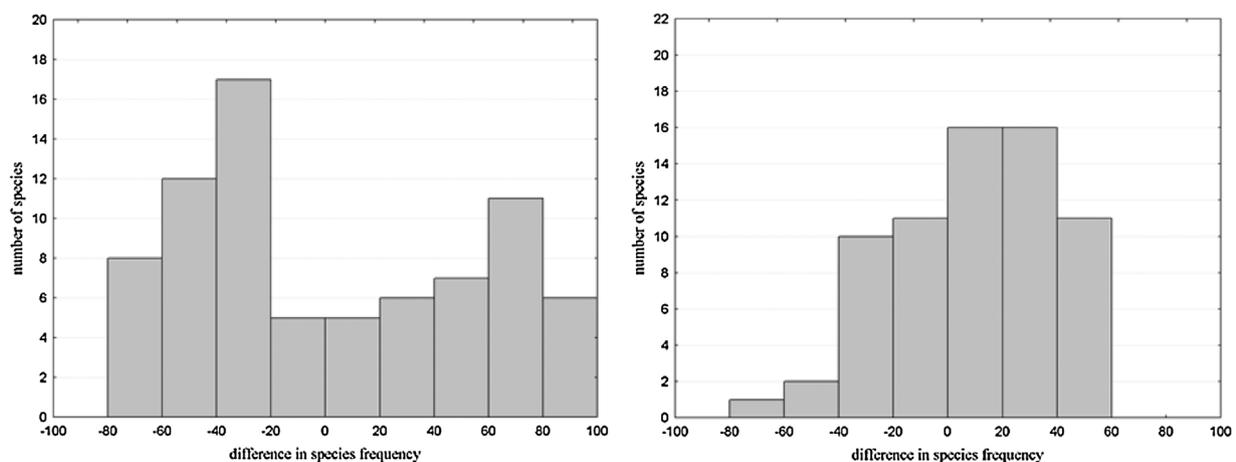
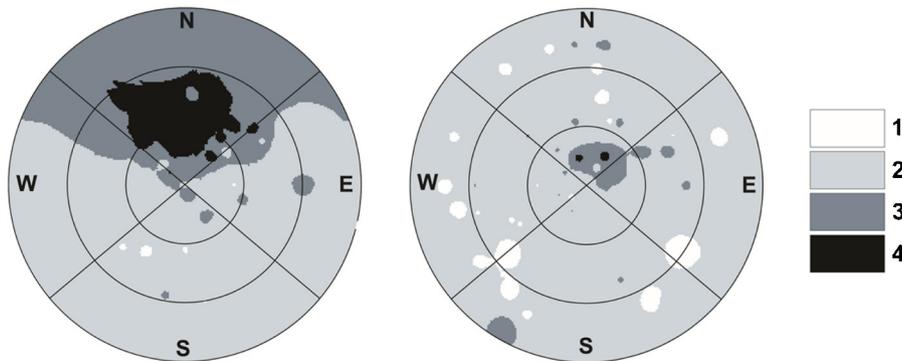


Fig. 2. The pattern for distribution of plant species frequency differences between opposite slopes at the Torey (left) and Dyrestuy (right) sites. Species with a frequency less than 30% were neglected.

**Table 4**  
Statistical comparisons of the indicator values for moisture between the Torey and Dyrestuy sites.

Mean Group 1South	Mean Group 2North	t-Value	df	p	Valid N Group 1	Valid N Group 2	Std. dev. Group 1	Std. dev. Group 2	F-ratio Variances	P Variances
Torey site 50.0684	56.9677	−15.0164	52	0.0000	33	21	1.7434	1.4765	1.3942	0.4394
Dyrestuy site 50.6820	49.9070	1.2369	51	0.2218	32	21	2.6165	1.4429	3.2882	0.0071



**Fig. 3.** The hill models for vegetation at the Torey (left) and Dyrestuy (right) sites. The outer circle reflects low slopes ( $<5^\circ$ ), the middle ring represents slopes of 5–15°, and the inner circle reflects steep slopes ( $>15^\circ$ ). The colors correspond to calculated IVM levels and typical vegetation: 1 (white) 44–48 – very dry habitats occupied by dry steppes, xerophytes (mostly bunchgrass) dominant in plant communities and represent the main part of the species pool; 2 (light grey) 48–52 – dry sites with typical bunchgrass steppe with abundant herbs, plant communities are formed mainly by xerophytes and subxerophytes; 3 (dark grey) 52–56 – relatively well-moisturized habitats, but moisture conditions are not stable (habitats regularly suffer from drought), with meadow steppes rich in subxerophytes; 4 (black) 56–60 – relatively well-moisturized habitats with meadows and grassy xeromesophytic forests formed by mesophytes and subxerophytes.

The hill models created for vegetation at the Torey and Dyrestuy sites (Fig. 3) clearly reflected the ecological patterns mentioned above, including the results of the IVM analysis. Distribution of the moisture within the Torey site was distinctly connected to the aspect. The Torey site demonstrated strong negative and significant correlations between the “southness” and the IVM ( $r = -0.8877$ ,  $p \ll 0.0001$ ;  $r_s = -0.7648$ ,  $p \ll 0.0001$ ). The Dyrestuy site was characterized by relatively monotonous moisture distribution, regardless of aspect ( $r = -0.0340$ ,  $p = 0.8130$ ;  $r_s = 0.2581$ ,  $p = 0.0674$ ). All habitats within this site were in the same range of moisture supply.

The correlation between the species composition similarity and IVM dissimilarities was calculated for both sites using the Mantel’s test. This correlation demonstrated the relationships between species composition and the wetness factor. The strong correlation ( $R_m = 0.6643$ ,  $p \ll 0.0000$ ) between the variables was revealed at the Torey site. This may be a consequence of wetness as the main limiting factor for vegetation in the typical larch forest-steppe landscape. On the other hand, the correlation between species composition and habitat wetness at the Dyrestuy site was much lower ( $R_m = 0.1549$ ,  $p = 0.0225$ ).

#### 3.4. Test of soil moisture assessment with field measurements

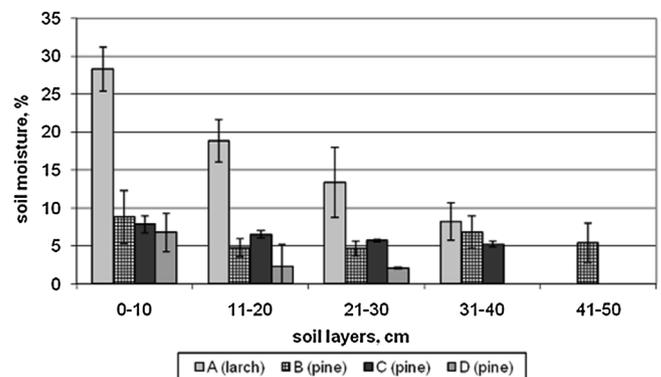
Results on the low level of topographical IVM differences in Dyrestuy were supported by the analysis of synoptic moisture measurements. No correlation was found between IVM and the directly measured air humidity ( $n = 22$ ;  $r = -0.1882$ ,  $p = 0.4016$ ;  $r_s = 0.0595$ ,  $p = 0.7926$ ). The latter was volatile and should be considered objectionable for using as a tool for habitat wetness assessment. The directly measured soil-moisture content was more stable and definitely reflected the differences between the larch and pine stands (Fig. 4). However, there were no significant dissimilarities found among the pine stands in the different areas of southern Siberia (Fig. 4). Nevertheless, these single measured data points give only relative estimations of the soil-moisture content and do not

provide an understanding of the mean moisture supply values that are typical for these habitats.

## 4. Discussion

### 4.1. Determinants of soil moisture patterns

Using indirect approaches, we assessed soil-moisture conditions in the contrasting larch forest-steppe environments and compared the data to the relatively homogenous pine forest-steppe landscape. It was established that soil wetness, redistributed by relief, was the significant environmental factor for forest-steppe vegetation where larch woodlands occupy the northern slopes. It is known qualitatively that soil moisture is connected with exposure, inclination, elevation, etc. (e.g. Lavelle and Spain, 2005; Seibert et al., 2007). The pattern of larch forest-steppe represented as sharply differentiated combinations of forest stands and steppe



**Fig. 4.** The relative soil-moisture content along the horizons in larch and pine woodlands. Localities of larch and pine woodlands are specified on the Fig. 1 (A, B, C, D).



communities corresponded to the aspect suggests that soil wetness is a likely important factor influencing plant community composition and spatial structure of vegetation. The larch forest–steppe was situated in the transitional zone between the humid boreal forest zone on one side and semi-arid steppe landscape on the other side. In this fashion, the larch forest–steppe represented a typical ecological community where the components of adjacent zonal ecosystems were combined (Anenkhonov et al., 2008; Kharuk et al., 2010).

The mean wetness differences between the northern and southern slopes at the Torey site were sufficiently high reaching approximately seven levels. To specify, it is known (Korolyuk, 2008) that the difference of four levels corresponds to the average wetness differences between the steppe plant communities of the subzonal level. The mean values of both the northern and southern slopes at the Torey site corresponded to the wetness levels in a species-rich bunch-grass steppe, as Tsatsenkin et al. (1974) established for the whole area in Siberia.

Significant hydrothermic differences between forest–steppe habitats, corresponding to the aspect have been revealed. Namely evaporation is known to decrease with slope inclination on shady slopes, and increase with inclination on the sunny slopes in settings similar to the areas studied here (Liu et al., 2012). Due to this, it is likely that the sunny slopes existed in a soil–water deficit and relatively sparse steppe communities with coverage from 30 to 60% probably developed for this reason. In our study, the grass layer was not substantially shading the ground surfaces in these communities, most likely facilitating the drying of the upper soil horizons. The reverse situation probably occurred on the shady slopes: decreased insolation and a sufficient soil water supply almost certainly enabled the development of larch forest communities. Additionally, the multiple-storey forest structure possibly provided additional decreasing physical evaporation. In such a case, plants are known to significantly influence ground heating and soil evaporation (e.g. Breshears et al., 1998; Raz-Yaseef et al., 2010). Consequently, it seems highly likely that vegetation is able to further strengthen the microclimatic peculiarities of northern slopes in regions like those under study here.

The forest–steppe landscape with the pine woodlands in Dyrestuy clearly differed from the forest–steppe with larch in Torey due to a soil moisture deficiency. In drier conditions, the soil properties of the gravel and stone content probably became important factors affecting the community distributions, as was previously known for Scots pine forests confined to sandy, as well as to rocky habitats (Rysin and Savel'eva, 2008; Milyutin et al., 2013). Because of soils at the Dyrestuy site were often with textures of sand, gravel, or stone, the vegetation spatial patterns very likely were affected not only by moisture content, but also by soil traits. In particular, the Scots pine formed woodlands mostly on the shady slopes, but did not totally dominate these sites. It was identified in approximately 28% of the relevés collected in forests along the northern slopes, reflecting a wide distribution of steppe vegetation (72% of the relevés along the northern slopes) around the forest patches. In general, xerophytic perennial herbs and a small portion of xerophytic annuals and dwarf shrubs primarily composed the local forest–steppe communities.

Differences between soil moisture in the larch and pine woodlands were effectively recognized using the plant species composition as a determinant of the wetness condition throughout the range of habitats. Specifically, the wetter conditions among the forest–steppe communities were revealed in the larch woodlands.

#### 4.2. Vulnerability of pine forests to drought in the forest–steppe in southern Siberia

There are different patterns of Scots pine vulnerability to drought across the area of its distribution. For instance, at the

southwestern distribution limit of Scots pine (Iberian Peninsula), increasing droughts resulted in a higher mortality rate for the pine trees. This phenomenon was described as the process of large-scale self-thinning of Scots pine forests appeared to be enhanced by dry conditions (Vilà-Cabrera et al., 2011). Scots pine trees in temperate forests that are positively influenced by warm and wet conditions during the previous December were vulnerable to temperature and soil water deficits during the growing season (Michelot et al., 2012). The radial growth in Scots pine trees were strongly limited by high summer temperatures and low summer precipitation in smaller trees in contrast to larger trees. During dry years, however, larger pine trees exhibited stronger growth reductions (Zang et al., 2012). Studies on the regeneration of Scots pine and encroachment onto the steppe at the forest–steppe ecotone in northern Mongolia revealed that the distribution of this species was very limited, and was mostly restricted to the immediate vicinity of the forest (Dulamsuren et al., 2013).

Eilmann et al. (2011) concluded that Scots pine trees under drought stress build a more effective water-conducting system (larger tracheids). As a result, pine trees are relatively tolerant to dry conditions, and can grow near the water limit of forests. Particularly, in southern Siberia, the Scots pine forests grow in variable environments, including areas dry enough to be comparable to the dry steppe conditions (Milyutin et al., 2013). Nevertheless, a significant shortening of the growth period as well as lower growth rates has been demonstrated in pine trees under drought conditions (Eilmann et al., 2011; Sanchez-Salguero et al., 2012). Moreover, at the southern edge of its distribution, which was defined by temperature and wetness, Scots pine has been shown to be vulnerable to fire. In such cases, other forests or shrublands could replace the Scots pine (Vilà-Cabrera et al., 2012). All in all, there are numerous pieces of evidence indicating an enhanced die-off risk for Scots pine in the case of frequent and severe droughts under expected warmer and drier conditions sometime in the future (Sanchez-Salguero et al., 2012). Although *P. sylvestris* has been demonstrated to be sensitive to the moisture shortage, it does not exhibit drought-induced mortality in southern Siberia (Kasyanova, 2004). The reason for this was that *P. sylvestris* was able to survive by means of reducing the transpiration intensity up to a minimal level. Thus, Scots pine, along with sensitivity to the moisture shortage, was characterized by high tolerance to this stress factor. Based on those assumptions, we can conclude that Scots pine forests are quite resilient to increases in climate aridity.

#### 4.3. Vulnerability of larch forests to drought in the forest–steppe in southern Siberia

Compared to Scots pine, resilience of the Siberian larch to drought has been poorly studied. According to scattered data in Russian literature, Siberian larch is well adapted to severe climates and is confined to areas with MAP 300–450 mm (e.g. Koropachinskii and Vstovskaya, 2002), where strong droughts are abnormal events. In the study area, the larch forests had some resistance to drought, but were also sensitive to soil–moisture conditions (Vipper, 1968). In more arid regions, Siberian larch no longer occurred, suggesting that this species is not tolerant to strong moisture shortages. Moreover, in neighboring northern Mongolia (along the southern edge of the Siberian boreal system), *L. sibirica* often suffer from drought stress, even under the current climate (Dulamsuren et al., 2009). Our data from the southern Trans-Baikal region generally supported this conclusion (Wu et al., 2012; Liu et al., 2013). Recent studies in northern Mongolia showed the growth reduction of *L. sibirica*, influenced by the increasing aridity during the 20th century (Dulamsuren et al., 2010a,b). In addition, the predicted progressive increase in aridity during the 21st century for western Khentey suggests a future decline of larch forests (Dulamsuren et al., 2010a).

Modeling of the main processes within the larch forests in eastern Siberia has revealed that soil water supply is a determinant influencing evapotranspiration and CO<sub>2</sub> fluxes. In dry years, the root access to soil-thawed water alleviates the soil water deficit (Park et al., 2011). In the forest-steppe of the western Baikal coast, the transpiration intensity in *L. sibirica* leaves has been shown to vary between 0.06 and 0.54 g g<sup>-1</sup> h<sup>-1</sup> (Kasyanova, 2004). This characterized less resilience of Siberian larch to the soil moisture shortage compared to Scots pine. In general, Siberian larch forests seem to be well adapted to a semi-arid climate, but not sufficiently tolerant to drought events and consistent increased aridity.

#### 4.4. Comparative vulnerability to drought between Scots pine and Siberian larch forests

Habitat wetness between Siberian larch and Scots pine forests distinctly differed, as indicated by the IVM of field-layer plants. In particular, in the semi-arid southern Siberia area, Scots pine was confined to dryer habitats compared to Siberian larch. Consequently, the pine trees faced more severe drought stress, unlike Siberian larch. Seeing that the larch forests were confined to more wet conditions compared to pine, and taking into account the data mentioned above, we suggest that these forests could be sustainable when climate is relatively stable. However, increasing aridity will cause increasing dryness in all habitat ranges. In this case, larch forests undoubtedly will become increasingly vulnerable, while pine forests will appear to be more sustainable. This is probably the reason for potential replacement of grassy larch forests by pine forests in dryer sites at the study area, along with increases in aridity projected in the region. As a result, in the future it is likely that more tolerant pine forests will represent forest patches in the forest-steppe landscape and monotony of the landscape will increase. Thus, within the set of all possible outcomes of this process, the loss of forest-steppe typological diversity will become especially noticeable.

#### 4.5. General considerations and implications

Our results show that indirect assessment of moisture conditions in the forest-steppe habitats using vegetation was preferable to synoptic or single-shot measurements. The lack of long-term observations is a primary reason why indirect assessment provides a unique way to explore landscape ecology as plant communities integrate environmental conditions over time. Moreover, this approach provides an opportunity to classify landscapes according to soil humidity level, and from this approach, we can analyze the spatial structures of vegetation and in some cases examine its vulnerability with regard to wetness factors.

Increasing aridity will inevitably lead to forest decline in the forest-steppe, along with subsequent changes in the typological and spatial patterns of the landscape. These changes may cause variable alterations in the ecosystem's functioning, potentially influencing the local economies. In this case, assessment of potential threats becomes an important concern. At the same time, tree species inhabiting forest-steppe landscapes differ in environmental preferences. This is the reason why various successional trajectories might occur, depending on response patterns of dominant plants and habitat qualities to the increases in drought stress. Because the forest-steppe feedback toward increasing aridity is complex and largely variable, approaches to the assessment of sustainability/vulnerability have still not been sufficiently developed. In general, a comprehensive analysis regarding autecological, as well as synecological traits of species should be carried out. Current environmental conditions and projected trends of climatic changes serve as basic assumptions in the course of such analyses. As a result, understanding habitat ecology in regard to plant

traits should support conclusions on the most probable responses of plants to climate-driven environmental changes. Based on the results of our study, analyzed together with available published data, we conclude that increasing aridity is highly likely to cause the replacement of Siberian larch by Scots pine in the southern Siberian forest-steppe landscape. In general, it means that the regional landscape may become more monotonous.

The combination of plant indicator values for soil moisture and empirical data on plant biology enables the selection of key species inhabiting ecosystems with different moisture conditions. These key species could represent sensitive indicators of long-term trends in soil moisture conditions that are reflective of changes in global precipitation and other climatic conditions. Furthermore, the ecotonal biomes, such as the forest-steppe, play an important role in regulating the ecosystem and landscape processes, and are potential indicators of climate change (Risser, 1993). Taking into account that ecotonal ecosystems are sensitive to various disturbances, including global climate change, plant communities of the forest-steppe are important systems for monitoring networks. Consequently, development of the practical methods for exploring the effects of habitat moisture, as described in this paper, are important for understanding the climate-forced dynamics of ecosystems.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2015.04.012>

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