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Edge effects on epiphytic lichen diversity in the forest-steppe of the Kazakh Altai

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Background: Forests in forest-steppe ecotones are usually highly fragmented and much of the forested area is exposed to climate and land-use-related edge effects.

Aim: To test the hypothesis that the epiphytic lichen diversity at the forest edges was reduced compared with that in the forest interior, and to analyse lichen diversity in comparison with the more highly elevated and more continental Mongolian Altai.

Methods: Six plots each in the interior and the edge with a total of 240 *Larix sibirica* trees were studied in the Katon-Karagai National Park, East Kazakhstan.

Results: Species richness and evenness at the tree level were higher in the interior than at the edge. The epiphytic lichen diversity in the forest interior was similar in the Kazakh and Mongolian Altai, whereas that at the forest edge was lower in the Mongolian Altai.

Conclusions: Strong degradation of the forest edges in the Kazakh Altai is the probable cause of the reduced epiphytic lichen diversity compared with the interior. The similar species richness in the forest interiors of the Kazakh and Mongolian Altai suggests that the differences at the forest edge are probably, at least partly, due to different land-use regimes and not to differences in macroclimate.

Keywords: alpha-diversity; Central Asia; evenness; forest grazing; nitrophytes; selective logging; Siberian larch (*Larix sibirica*); silver birch (*Betula pendula*)

Introduction

The diversity and ecology of epiphytic lichens in the Eurasian forest-steppes is notoriously under-researched (Hauck et al. 2013), though this vegetation type stretches almost 9000 km across the continents along the border of the forest and the steppe zones (Lavrenko et al. 1991; Walter and Breckle 1994). The number of published studies on epiphytic lichens from the forest-steppe is rather limited (e.g. Biazrov 1974; Sorokina 2001; Muchnik 2010). The Altai Mountains form an important biogeographic barrier between the Eurosiberian (Black Sea–Kazakhstan) steppe region, ranging from Eastern Europe to East Kazakhstan, and the Mongolian–Chinese (Central Asian) steppe region (Lavrenko and Karamysheva 1993). The Eurosiberian steppes differ strongly from comparable landscapes east of the Altai mountain range by their lower elevation, flatter landscape, higher temperature, higher and more evenly distributed precipitation as well as in their land-use history.

A typical character of forest-steppes is the high degree of fragmentation of the forest stands, which creates high ratios of edge to interior. Where the spatial distribution of forests is not primarily determined by land use, forests are mostly found on north-facing mountain slopes, whereas south-facing slopes and dry valleys are covered by grasslands (Walter and Breckle 1994; Gunin et al. 1999). Due to the high fragmentation, much of the total area of the forest stands is influenced by the steppe in terms of microclimate and the input of dust. Furthermore, the forests are impacted by human activities and livestock, as livestock keeping is a typical type of land use in the forest-steppe ecotones (Lkhagvadorj et al. 2013). Recent studies from the Mongolian–Chinese steppe region showed that epiphytic lichen diversity was strongly influenced by the intense solar irradiation, input of dust, fertilisation of trunk bases and abrasion of bark surfaces by grazing livestock, collection of deadwood for fuel and by the rarity of large-diameter trees due to selective logging (Hauck et al. 2007, 2012; Hauck and Lkhagvadorj 2013).

The objective of the present study was to analyse the epiphytic lichen diversity in the forest-steppe ecotone of the eastern Eurosiberian steppe zone, with the Kazakh Altai being selected as the study region for a case study. Many forests in eastern Kazakhstan have been strongly disturbed through logging during Soviet times, livestock grazing and fire (Meshkov et al. 2009). The forest edges especially are often heavily degraded and converted into shrublands. Many conifer stands have been replaced by birch forests after disturbance. The conversion of Kazakhstan's most productive grasslands into arable land during the 1950s increased the grazing pressure by livestock in the remaining areas, with steadily increasing livestock numbers from the 1930s to 1990 (Robinson and Milner-Gulland 2003). After Kazakhstan had become politically independent in 1991, livestock production declined (Suleimenov and Oram 2000; Robinson and Milner-Gulland 2003) and logging was reduced in many places (Kushlin et al. 2004; Meshkov et al. 2009), including the study area, which is located

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in a national park established in 2001. The objective of present paper is to analyse the present state of epiphytic lichen diversity after decades of forest degradation at a putative turning point to more sustainable forest utilisation in Kazakhstan. Since the forests are particularly degraded at their edges, the hypothesis was tested that species diversity at the forest edges was reduced in comparison with the forest interiors. Furthermore, the hypothesis was tested that the less harsh and more humid climate in the eastern Eurosiberian steppe zone than in the Chinese–Mongolian steppe would result in higher total species diversity in the Kazakh Altai than in the Mongolian Altai, where a published study with a similar sampling design as

applied in the present study was available for comparison (Hauck et al. 2012).

Materials and methods

Study area

Field work was carried out in the Katon-Karagai National Park in the province of East Kazakhstan in summer 2010 (Figure 1). The study sites were located at 1200–1400 m a.s.l. at the southern rim of the valley of the River Bukhtarma, east of the town of Katon-Karagai, between the villages of Chingistai and Enbek (Table 1). The forests of the sampling areas included stands of Siberian larch (*Larix*
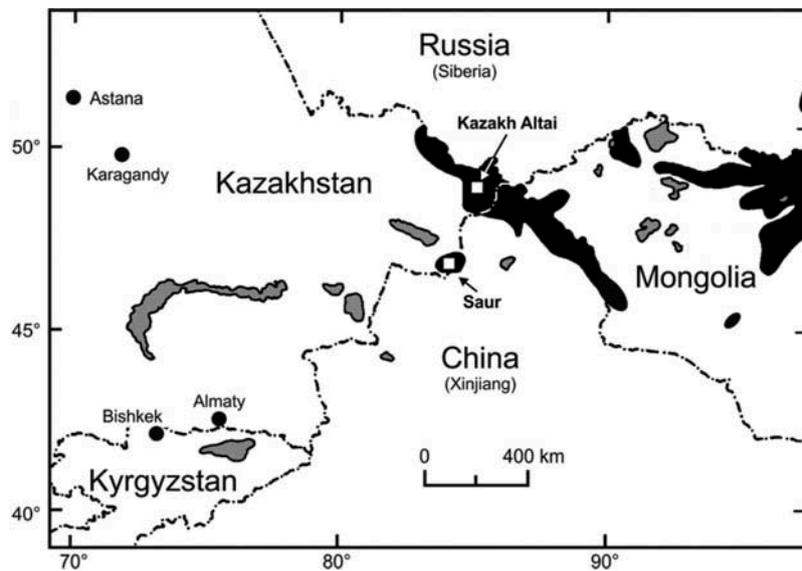

Figure 1.   Study areas (marked with white boxes) in the Kazakh Altai, East Kazakhstan. The black areas indicate the distribution of *Larix sibirica*-dominated taiga forests in Kazakhstan, China and Mongolia; the distribution of larch forests in Russia (entire map area in Russia falls in the distribution range of *L. sibirica*) is not shown for the sake of clarity. Grey areas are lakes.

Table 1.   Location and stand characteristics of the sample plots in the Kazakh Altai.

		Site					
	Habitat	1	2	3	4	5	6
Latitude (N)[a]		49° 9′ 36″	49° 8′ 59″	49° 9′ 8″	49° 8′ 30″	49° 8′ 39″	49° 8′ 31″
Longitude (E)[a]		86° 1′ 55″	85° 59′ 54″	86° 0′ 38″	85° 57′ 40″	85° 57′ 57″	85° 56′ 21″
Altitude (m a.s.l.)[b]		1365	1200	1260	1400	1310	1340
Canopy closure (%)	FI	30	30	30	45	30	20
	FE	30	30	25	15	40	20
Larix sibirica (%)	FI	15	30	30	45	30	18
	FE	30	20	20	15	35	20
Betula pendula (%)	FI	15	0	0	0	0	2
	FE	0	10	5	0	5	0
Shrub layer (%)	FI	45	70	75	70	85	70
	FE	20	70	75	75	50	70
Trees with DBH ≥ 40 cm	FI	2	0	1	1	1	4
	FE	7	0	0	14	5	6
Trees with DBH ≥ 50 cm	FI	1	1	0	0	1	0
	FE	4	0	0	10	3	1

FE, forest edge; FI, forest interior.
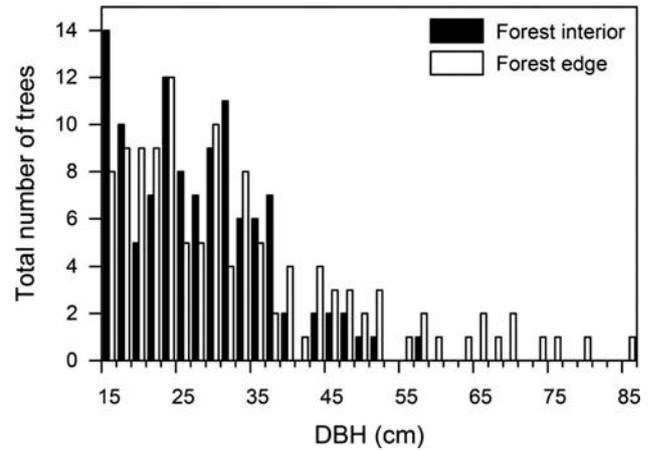[a]Specifications refer to the sample plot at the forest edge.

Figure 3. Distribution of tree diameter classes in the studied larch stands ($N = 240$ trees) in the forest interior and forest edge in the Altai Mountains, eastern Kazakhstan. The diameter at breast height (DBH) is divided into classes of 2 cm, with the labels of the axis of abscissas indicating the lower limit of the individual classes.

encloses the lower 1–1.5 m of the tree trunks. The forest edges in particular are often heavily degraded (Figure 2(a) and (b)) and possess a gap-rich canopy with low cover (between 15–40%). The stem diameter distribution of the larch trees in studied stands (Figure 3) shows that the natural reverse J-shaped distribution has been considerably disturbed. This concerns the rarity of large-diameter trees (especially in the forest interior), but also the periodic under-representation of lower-diameter classes, which are likely to represent events of selective logging.

The climate in the study area is strongly continental. Mean annual precipitation at the nearest weather station in Katon-Karagai (49°10′58″ N, 85°37′1″ E, 1081 m a.s.l.) between 1940–2010 was 447 mm. Mean temperatures were 1.7 °C for the whole year, 16.5 °C in July and −13.4 °C in January. Monthly means of temperature and precipitation are shown in Figure 4 in comparison with data from the Mongolian Altai in the Mongolian-Chinese steppe zone.

Today, the steppe and forest margins of the study area are subjected to moderate grazing by cattle, horses, sheep and goats by local herders, who are partly sedentary in nearby villages and partly conduct transhumant livestock herding. Horses and cattle penetrate much deeper into the forests than goats and sheep.

Sample plot selection

Six north-facing forest stands were selected at the southern rim of the Bukhtarma Valley. The sites (stands) were selected at a mean distance of 1.6 ± 0.4 km from each other. The sites could not be chosen randomly, because we intended to select monospecific stands of Siberian larch or at least stands which were strongly dominated by larch. Many forest stands in the forest-steppe ecotone of the study area had apparently been subjected to heavy disturbance in the past and were dominated by birch. Relatively moist depressions, which occur locally on the mountains slopes,

Figure 2. Forests, edges in particular, are often strongly degraded in the Kazakh Altai. Edge of a *Larix sibirica* forest, partly degraded to shrubland (a); example of forest edge plot with canopy gaps, trees of *Betula pendula* which are sporadically intermixed with larch and a dense shrub layer (b); example of forest interior plot with dense shrub layer (c).

sibirica Ledeb.), which partly became mixed with silver birch (*Betula pendula* Roth) after disturbance (Figure 2). Many heavily disturbed sites were covered by pure birch forest. The larch forests of the area usually have a dense, nearly impenetrable shrub layer (Table 1) formed by species of *Spiraea*, *Rosa*, *Rubus*, *Ribes*, *Cotoneaster*, *Lonicera*, and *Crataegus* (Figure 2(b) and (c)). This shrub layer often
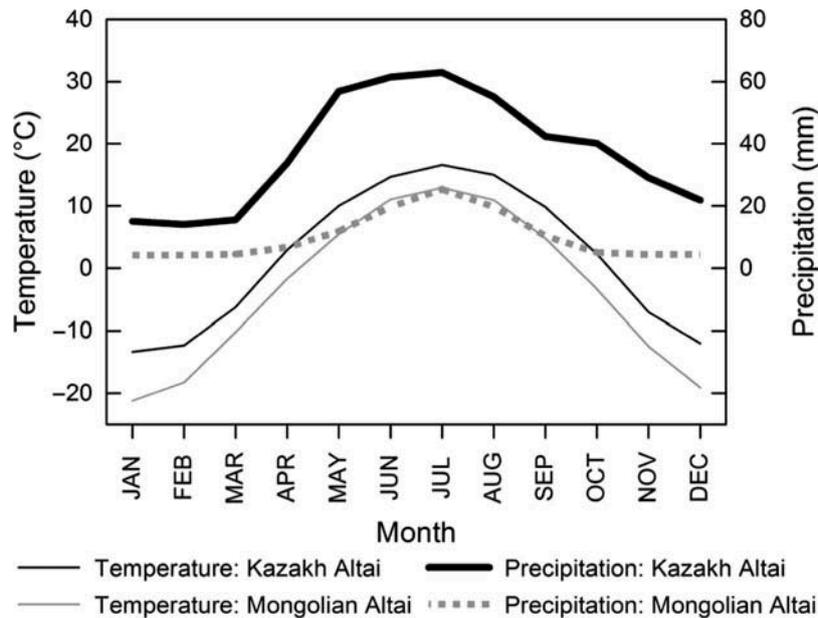
Figure 4.   Climate chart from the weather stations Katon-Karagai (49° 10′ 58″ N, 85° 37′ 1″ E, 1081 m a.s.l.) in the Kazakh Altai (Eurosiberian steppe region) and Altai, western Mongolia (48° 17′ N, 89° 31′ E, 2150 m a.s.l.) in the Mongolian Altai (Mongolian–Chinese steppe region), based on data from 1940–2010.

were avoided to improve the comparability among stands. At each site, two plots each of 20 m × 20 m size were selected. One plot was located at the forest edge with its downslope boundary coinciding with the forest-steppe boundary. The other one was located 50–100 m inside the forest. On average, the elevation of the interior plots was 78 ± 5 m a.s.l. higher than that of the edge plots. The forest edge was generally more sun-exposed, warmer and drier than the forest interior, but measurements from the study plots are unavailable. Two-thirds of the sample trees had a diameter at breast height (DBH) < 40 cm; 24% of the trees were > 40 cm and 9% of the trees had a DBH > 50 cm (Table 1).

Lichen data recording

Epiphytic lichen vegetation was studied on 20 larch trees per plot with a DBH of ≥ 15 cm. The 20 trees growing most closely to the lower edge of the plot were selected. On plots with less than 20 trees, additional trees, growing closest to the plot, were selected. In addition, 10 birch trees were studied each at the forest edge and in the forest interior of Site 1. On the other plots, birch was too rare for analysis or even absent.

On each sample tree, all individual lichen species were recorded on the trunks at a height of 0–2 m from ground level, including all aspects, i.e. the whole circumference of the trunk. The cover of each species was estimated in percentage. All cover values of < 1% were included as 0.5% in the data analyses. Coarse roots located above the soil surface were included in the investigated bark surfaces. On the larch trees the epiphytic lichens of the lower branches (0–2 m above the ground) were also recorded, but not quantified.

Nomenclature is based on Urbanavichus (2010), except for the Teloschistaceae (*Caloplaca* s.l., *Xanthoria* s.l.) where nomenclature follows Arup et al. (2013) and *Biatora chrysanthoides* Printzen & Tønsberg. The material called *Bacidina* spec. is probably *B. adastra* (Sparrius & Aptroot) M. Hauck & V. Wirth, but was not assigned to this species, because the lichen was always sterile and Central Asia is far from the presently known range of this species. *Cladonia pyxidata* s.l. includes *C. chlorophaea* and *C. grayi*, but not *C. pocillum*; this circumscription was chosen for practical reasons, although the latter is more closely related to *C. pyxidata* s. str. than *C. grayi* and probably also *C. chlorophaea*. *Rinodina* spec. refers to *R. septentrionalis* and perhaps other species; it does not include *R. exigua* and *R. pyrina* (det. H. Mayrhofer).

Data analysis

Arithmetic means ± standard errors are given throughout the paper. Since the data were mostly not normally distributed (Shapiro–Wilk test), data were tested for significant differences with Mann–Whitney's *U*-test. The grouping of sample trees in variation of the epiphytic lichen abundance was analysed with non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM). The calculation of NMDS was based on relative Euclidean distances. In comparison to the also widely used Bray–Curtis distances, Euclidean distances emphasise less the difference between the complete absence of a species and its occurrence with low abundance. Given the inconspicuousness and low abundance of many lichen species, we felt that this better met the requirements of our dataset. The goodness of the fit was assessed by calculating Kruskal's stress

1, which should be <20. A total of 250 iterations were run with both the real data and randomised data used for a Monte Carlo test. The ANOSIM was also calculated with Euclidean distances and included a Monte Carlo permutation test with 9999 iterations. The R value resulting from the ANOSIM is defined as $R = (r_B - r_W)/(N[N - 1]/4)$, with r_B and r_W being the mean between-group and within-group ranks and N being the number of samples; $R = \pm 1$ indicates perfect grouping, whereas $R = 0$ indicates random grouping (Clarke 1993). The effect of environmental parameters on the species data was analysed by using canonical correspondence analysis (CCA) followed by a Monte Carlo test with 999 permutations. Indicator species analysis after Dufrêne and Legendre (1997) was calculated to identify species which are characteristic of the forest interior, the forest edge and large- and small-diameter trees. The indicator species analysis was connected with a Monte Carlo permutation test with 4999 iterations. The diversity and the dominance structure of the studied epiphyte vegetation was analysed by calculating the total species richness (α-diversity) at the tree and plot levels, the species turnover between the forest interior and the forest edge (β-diversity) at the landscape level and the N_1-diversity (evenness) at the tree level. The β-diversity was defined as $\beta = \gamma/\alpha$, with γ being the total species diversity of the epiphytic lichens at all study sites, respectively. To analyse species dominance in the epiphytic lichen vegetation, N_1-diversity was calculated, which is defined as $N_1 = e^{H'}$ (Krebs 1999). In this equation, H' is the Shannon function:

$$H' = -\sum_{i=1}^{n} pi \times \ln pi$$

with pi = cover of species i divided by the total cover of all species per sample. N_1 specifies the number of equally abundant species producing the same diversity value as the calculated Shannon function H'. Large differences between N_1 and the total number of species (α-diversity) in a sample indicate the dominance of few species (i.e. reduction of plant diversity according to Shannon). Furthermore, the dominance structure of the epiphytic lichen vegetation was graphically analysed by plotting the cumulative log cover of each species versus its frequency on the sampled trees. For tree-level diversity indices, mean values were calculated for all trees in a plot and then the plot-wise means were used to calculate habitat-wise mean values for the forest interior and the forest edge. For analysing bivariate correlations, Pearson correlation coefficients were calculated.

NMDS and the CCA were computed with the program PC-Ord 5.14 (MjM Software, Gleneden Beach, Oregon, USA). ANOSIM was calculated with PAST 2.15 (Ø. Hammer, Natural History Museum, University of Oslo, Norway). All other statistical analyses were conducted with SAS 9.13 software (SAS Institute Inc., Cary, North Carolina, USA).

Results

The survey trunk surfaces (0–2 m above the ground) of the studied 240 larch trees harboured a total of 86 epiphytic lichen species (Table 2). A total of 59 species was found in the forest interior, whereas 70 species were recorded at the forest edge. The plot-level α-diversity (Figure 5(a)) was not different between the habitats, but the tree-level α-diversity (Figure 5(b)) was significantly higher in the forest interior (12.6 $\pm$ 0.8 species tree^{-1}) than at the forest edge (9.4 $\pm$ 0.4 species tree^{-1}). The plot-level α-diversity increased with increasing tree-level α-diversity in the forest interior ($r = 0.83$, $P = 0.03$; $y = 2.79x - 3.85$), but not at the forest edge. The β-diversity (Figure 5(c)) exhibited a slight insignificant tendency for higher values in the forest interior than at the edge. The tree-level N_1-diversity (Figure 5(d)) was significantly higher in the forest interior, which corresponded to the higher α-diversity in this habitat.

The results of the NMDS (Figure 6) suggested a significant difference of the epiphytic lichen vegetation of the larch trunks between the forest interior and the forest edge (along the second axis of the ordination space), but also showed a considerable overlap between these habitats. The results of the NMDS agreed well with that of the ANOSIM, which was highly significant ($P < 0.001$), but had a small r value ($r = 0.13$). Assessed from frequency and cover values, more species had a preference for the forest interior than for the forest edge (Table 2). Some 19% of the species (16 species) had significantly ($P \leq 0.05$) higher frequency and/or cover values on the larch trees of the forest interior than on trees at the forest edge, but in only 11% (nine species) of the total species it was the other way round. A further nine species, however, had a trend for higher abundance at the forest edge which was marginally significant ($P \leq 0.10$), whereas the opposite trend was only observed for *Usnea* sp. Nine species, which occurred on > 1% of the sample trees, did not show a significant preference for either habitat. Some 49% (41 species) of the total species had no significant test result either, but were too rare (frequency < 1%) to deduce ecological indifference to the habitat from this result. Species with significant preference for the forest edge had generally lower P values in the U-tests for frequency and cover than species with preference for the forest interior. Pertaining to frequency, P was ≤ 0.01 in nine species with preference for the forest edge, but in only four species with preference for the interior; for cover, values were similar with nine and five species, respectively. Indicator species analysis revealed 17 species as significant indicators of the forest interior and eight species as indicators of the forest edge (Table 3).

The cover of most lichen species was clearly < 1%; only *Parmelia sulcata* and *Cyphelium tigillare* inhabited substantially larger areas of the trunk bases. If cover of the individual species was accumulated over all sample trees, it was usually proportional to the frequency of the relevant lichen species (Figure 6). However, ca. 10 species at the forest edge and five species from the

Table 2.   Mean frequency and cover (in percent ± SE) of lichen species occurring with a mean frequency of > 1% in the forest interior (FI) or the forest edge (FE) on the trunks of *Larix sibirica* in the Kazakh Altai.

	Frequency			Cover		
	FI	FE	P^a	FI	FE	P^a
Species with higher frequency and/or cover in the forest interior:						
Parmeliopsis ambigua	73 ± 6	20 ± 6	0.003	0.4 ± 0.1	0.1 ± 0.0	0.003
Cladonia coniocraea	42 ± 10	4 ± 2	0.003	0.2 ± 0.1	0.0 ± 0.0	0.003
Hypogymnia austerodes	67 ± 8	23 ± 5	0.004	0.3 ± 0.1	0.1 ± 0.0	0.005
Flavopunctelia soredica	23 ± 8	5 ± 3	0.004	0.1 ± 0.0	0.0 ± 0.0	0.04
Vulpicida pinastri	79 ± 8	35 ± 4	0.005	0.3 ± 0.1	0.1 ± 0.0	0.005
Hypogymnia physodes	73 ± 8	27 ± 8	0.005	0.7 ± 0.2	0.1 ± 0.0	0.007
Cladonia pyxidata s.l.	50 ± 11	10 ± 4	0.006	0.2 ± 0.1	0.0 ± 0.0	0.003
Chaenotheca stemonea	29 ± 13	1 ± 1	0.01	0.2 ± 0.1	0.0 ± 0.0	0.01
Chaenotheca trichialis	15 ± 7	–	0.01	0.1 ± 0.1	–	0.01
Pseudevernia furfuracea	69 ± 9	38 ± 8	0.02	0.3 ± 0.1	0.2 ± 0.0	0.10
Bryoria fuscescens	52 ± 9	26 ± 7	0.02	0.2 ± 0.0	0.1 ± 0.0	0.02
Lecidella euphorea	58 ± 8	33 ± 8	0.03	0.2 ± 0.0	0.1 ± 0.0	0.05
Cyphelium tigillare	74 ± 11	–	0.04	2.9 ± 0.7	2.3 ± 0.7	
Arthonia mediella	4 ± 2	–	0.04	0.0 ± 0.0	–	0.04
Lecanora varia	68 ± 8	48 ± 7	0.05	0.3 ± 0.1	0.2 ± 0.0	
Parmelia sulcata	99 ± 1	92 ± 5		6.5 ± 0.9	1.5 ± 0.2	0.003
Usnea spec.	95 ± 2	90 ± 8		0.6 ± 0.1	0.4 ± 0.0	0.09
Species with higher frequency and/or cover at the forest edge:						
Physcia adscendens	1 ± 1	18 ± 5	0.003	0.0 ± 0.0	0.1 ± 0.0	0.003
Polycauliona candelaria	6 ± 2	33 ± 8	0.006	0.0 ± 0.0	0.5 ± 0.4	0.01
Candelariella reflexa	1 ± 1	16 ± 5	0.01	0.0 ± 0.0	0.1 ± 0.0	0.01
Lecanora hagenii	–	6 ± 3	0.01	–	0.1 ± 0.1	0.01
Physcia dubia	7 ± 4	30 ± 8	0.02	0.0 ± 0.0	0.3 ± 0.1	0.002
Physcia stellaris	28 ± 8	63 ± 10	0.03	0.1 ± 0.0	0.4 ± 0.1	0.02
Phaeophyscia orbicularis	–	4 ± 2	0.04	–	0.1 ± 0.0	0.04
Cladonia pocillum	–	3 ± 2	0.04	–	0.0 ± 0.0	0.04
Physciella chloantha	–	3 ± 1	0.04	–	0.0 ± 0.0	0.04
Lecanora albellula	32 ± 10	59 ± 13	0.07	0.6 ± 0.4	1.5 ± 0.5	
Candelariella aurella	–	5 ± 4	0.09	–	0.0 ± 0.0	0.09
Xanthomendoza ulophyllodes	–	4 ± 3	0.09	–	0.0 ± 0.0	0.09
Bacidina spec.	–	3 ± 2	0.09	–	0.0 ± 0.0	0.09
Aspicilia cinerea	–	3 ± 2	0.09	–	0.0 ± 0.0	0.09
Lecanora subintricata	–	3 ± 2	0.09	–	0.0 ± 0.0	0.09
Anaptychia ulotrichoides	–	2 ± 1	0.09	–	0.0 ± 0.0	0.09
Caloplaca cerina	–	2 ± 1	0.09	–	0.0 ± 0.0	0.09
Melanohalea elegantula	1 ± 1	3 ± 1		0.0 ± 0.0	0.0 ± 0.0	0.09
Species without significant difference for frequency or cover[b]:						
Melanohalea exasperatula	57 ± 13	63 ± 6		0.2 ± 0.0	0.4 ± 0.0	
Amandinea punctata	50 ± 10	40 ± 5		0.2 ± 0.1	0.2 ± 0.2	
Evernia mesomorpha	15 ± 5	13 ± 2		0.0 ± 0.0	0.0 ± 0.0	
Hypogymnia tubulosa	28 ± 11	11 ± 5		0.1 ± 0.0	0.0 ± 0.0	
Physconia enteroxantha	3 ± 3	10 ± 5		0.0 ± 0.0	0.0 ± 0.0	
Hypocenomyce scalaris	8 ± 4	5 ± 4		0.0 ± 0.0	0.1 ± 0.1	
Rinodina exigua	8 ± 3	5 ± 3		0.0 ± 0.0	0.0 ± 0.0	
Rinodina spec.	4 ± 3	4 ± 2		0.0 ± 0.0	0.0 ± 0.0	
Buellia spec.	5 ± 4	1 ± 1		0.0 ± 0.0	0.0 ± 0.0	

[a] *U*-test (df = 1); difference significant at $P \leq 0.05$, marginally significant at $P \leq 0.10$.
[b] Rare species (mean frequency < 5%) without significant test result; in brackets: mean frequency in the forest interior, forest edge: *Athallia pyracea* (0.0, 0.3), *Biatora* cf. *chrysanthoides* (0.8, 0.0), *Buellia erubescens* (0.0, 0.8), *Calicum viride* (1.7, 0.0), *Caloplaca monacensis* (0.0, 0.8), *Candelaria concolor* (0.0, 0.8), *Candelariella vitellina* (0.0, 0.8), *C. xanthostigma* (0.0, 0.8), *Chaenotheca furfuracea* (0.8, 0.0), *C. gracilenta* (0.8, 0.0), *Chrysothrix candelaris* (0.8, 0.0),*Coenogonium pineti* (0.0, 0.8), *Collema nigrescens* (0.0, 0.8), *C. subflaccidum* (0.0, 1.7), *Cyphelium notarisii* (0.8, 0.0), *C. pinicola* (0.8, 1.7), *Flavocetraria cucullata* (1.7, 0.8), *Hypogymnia bitteri* (3.3, 1.7), *H. farinacea* (0.8, 0.0), *Lecanora cadubriae* (2.5, 0.0), *L. chlarotera* (2.5, 0.8), *L. impudens* (0,8, 0,8), *L. pulicaris* (3.3, 0.8), *L. saxicola* (0.0, 0.8), *Lecidella scabra* (0.0, 0.8), *Lepraria elobata* (0.8, 0.0), *Lepraria jackii* (4.2, 0.8), *Leptogium saturninum* (0.0, 1.7), *Megaspora verrucosa* (0.0, 0.8), *Melanohalea exasperata* (0.8, 2.5), *Micarea prasina* s.l. (0.8, 0.0), *Parmeliopsis hyperopta* (0.8, 0.0), *Peltigera didactyla* (0.0, 1.7), *Physcia caesia* (0.8, 1.7), *P. tenella* (0.0, 0.8), *Rhizoplaca chrysoleuca* (0.0, 0.8), *Rinodina pyrina* (2.5, 0.8), *Rusavskia elegans* (0.0, 1.7), *Tetramelas triphragmoides* (0.8, 0.0), *Trapeliopsis flexuosa* (0.8, 0.0), *T. granulosa* (1.7, 0.0), *Xanthoparmelia stenophylla* (0.8, 0.8).
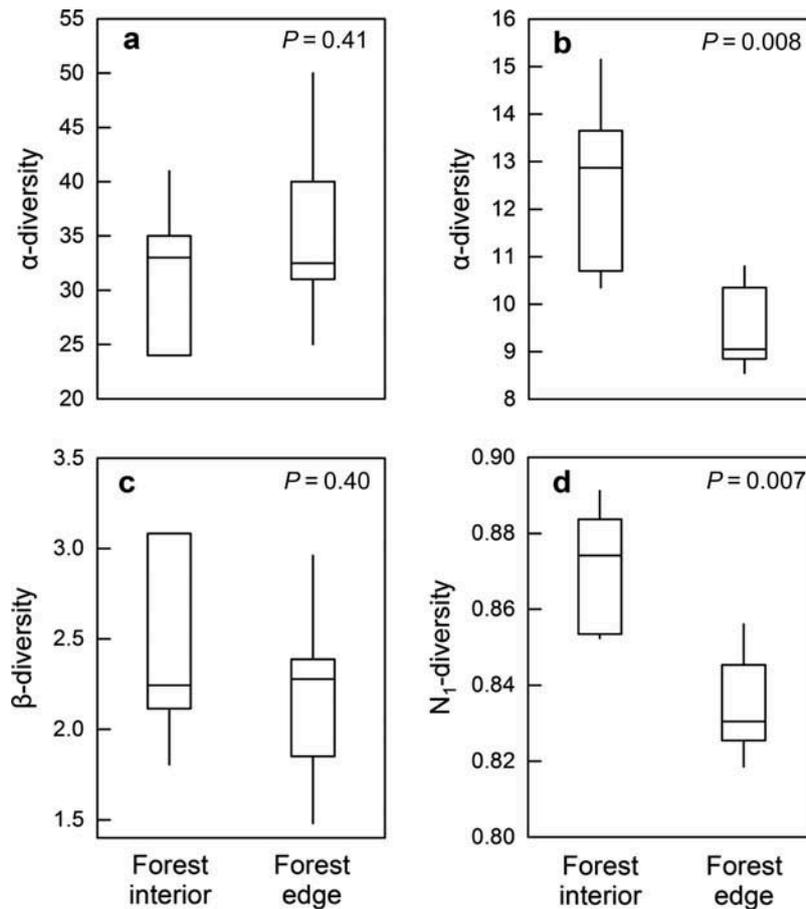
Figure 5. Epiphytic lichen diversity in the interior and at the edge of larch forests: total number of species (α-diversity) at the (a) plot and (b) tree levels; species turnover between the forest interior and the forest edge (β-diversity) at the landscape level (c); N_1-diversity at the tree level (d). Boxplots show medians, 25% and 75% quartiles as well as minima and maxima ($N = 6$). *P*-values represent the level of significance of *U*-tests.

forest interior deviated from this rule and had cumulative cover values over all sampled larch trees that were disproportionally high compared with their frequency. This applied to *Cyphelium tigillare*, *Lecanora albellula* and *Parmelia sulcata* in both habitats, *Chaenotheca stemonea* and *Hypogymnia tubulosa* in the forest interior as well as *Polycauliona candelaria* (= *Xanthoria c.*, *Massjukiella c.*), *Physcia dubia*, *Phaeophyscia orbicularis*, *Physconia enteroxantha*, *Lecanora hagenii*, *Melanohalea elegantula*, and *Cyphelium pinicola* at the forest edge.

Species richness on the trunks of the larch trees depended on stem diameter. However, the linear correlation of stem DBH with the tree-level α-diversity was only significant at the forest edge ($r = 0.37$, $P \leq 0.001$, $y = 0.11x + 5.77$), where the range of DBH was higher than in the forest interior (Figure 3). Remarkably, the indicator species analysis indicated only one species which was characteristic of trees with a DBH < 40 cm and 17 species as indicators of large-diameter trees with DBH ≥ 40 cm or ≥ 50 cm, respectively (Table 4). Except for *Melanohalea exasperata*, no lichen species occurred more frequently on the branches than on the trunks of larch, whereas many species preferred the trunk over the branches. The most frequent epiphytes of larch branches included *Melanohalea*

exasperatula (on 16% of the sample trees), *Parmelia sulcata* (15%), *Lecidella euphorea* (9%), *Lecanora albellula* (6%), *Melanohalea exasperata*, *Lecanora varia*, *Cyphelium tigillare* (5%), and *Hypogymnia austerodes* (4%).

At Site 1, where birch trees were present in addition to larch, the CCA demonstrated that tree species exerted a higher influence on epiphytic lichen vegetation than habitat or stem diameter (Table 5). This result was supported by the results of the ANOSIM, showing that the epiphytic lichen vegetation was significantly different between larch and birch ($R = 0.53$, $P < 0.001$). Characteristic species of birch, which were more frequent on this species than on larch, included *Arthopyrenia punctiformis*, *Melanohalea exasperata*, *Athallia pyracea* (= *Caloplaca p.*), *Candelariella aurella*, and *Hypogymnia tubulosa* (Table 6). *Arthopyrenia rhyponta* was also found on birch; this species showed no significant test result because of rarity, but was not expected to occur on larch trees.

Discussion

The epiphytic lichen vegetation in the larch-dominated forest-steppe of the Kazakh Altai was markedly different between the forest interior and the forest edge. In
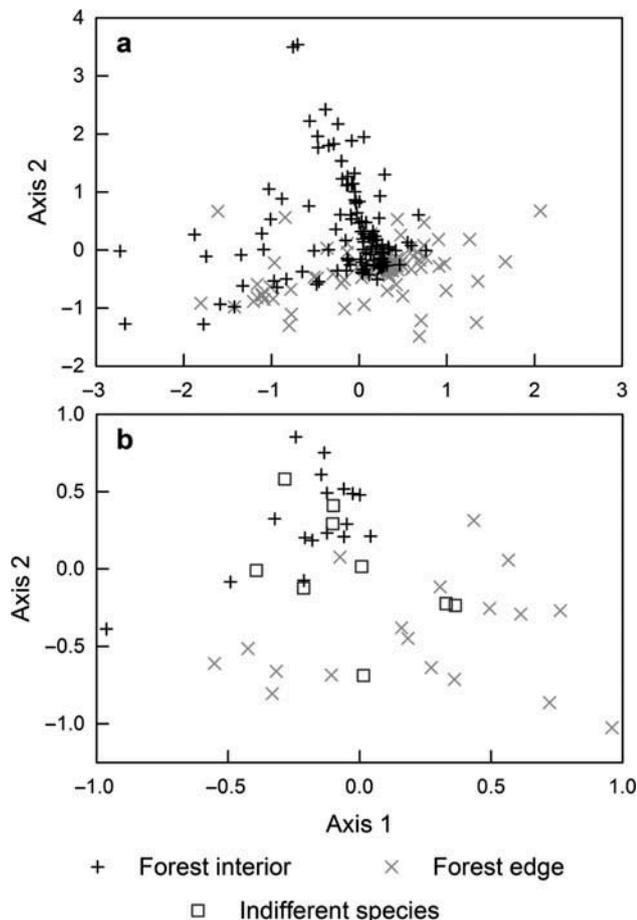
Figure 6. NMDS ordination of *Larix sibirica* trees ($N = 240$) growing in the forest interior or at the edge to the steppe in the Kazakh Altai depending on the individual cover values of the epiphytic lichen species ($N = 87$) occurring on the lower 2 m of the trunks: (a) trees, (b) species listed in the main body of Table 1 as being more frequent in the forest interior or the forest edge or indifferent to the habitat. Note different scales in (a) and (b) to improve resolution in (b). Final stress: 9.65 ($P = 0.02$, Monte Carlo test).

accordance with the first hypothesis, more species preferred the forest interior over the edge than the other way round. Moreover, the mean species richness (α-diversity) was higher in the interior than at the edge. However, this was only valid at the tree level, whereas the total number of species at the plot level was not different between the edge and the interior. In general, there does not appear to be a uniform response of epiphytic lichen diversity to edge–interior gradients. Rather, the effect of edge conditions on lichen diversity depends on land-use intensity, climate, atmospheric deposition of nutrients or toxic substances, gap size, and the functional traits of the relevant epiphyte species (Esseen and Renhorn 1998; Kivistö and Kuusinen 2000). Edge conditions are disadvantageous for those lichens which require high humidity and shade. This applies to oceanic specialists of humid forest interiors (Esseen 2006; Boudreault et al. 2008), but also less humidity-demanding species in semiarid woodlands (Belinchón et al. 2007). On the other hand, epiphytic lichens can benefit from the increased sunlight (Benson

Table 3. Indicator values (in % of perfect indication) resulting from indicator species analysis for trunk-inhabiting epiphytes of larch in the forest interior (FI) and the forest edge (FE).

	Indicator values (%)		
	FI	FE	P^a
Indicator species of the forest interior:			
Parmelia sulcata	81	17	<0.001
Hypogymnia physodes	63	4	< 0.001
Parmeliopsis ambigua	62	3	< 0.001
Vulpicida pinastri	59	9	< 0.001
Usnea spec.	54	39	0.005
Hypogymnia austerodes	52	5	< 0.001
Cladonia pyxidata s.l.	45	1	< 0.001
Pseudevernia furfuracea	45	13	< 0.001
Lecanora varia	41	19	0.003
Cyphelium tigillare	41	23	0.03
Cladonia coniocraea	40	0	< 0.001
Lecidella euphorea	38	11	< 0.001
Bryoria fuscescens	36	8	< 0.001
Chaenotheca stemonea	29	0	< 0.001
Hypogymnia tubulosa	21	3	< 0.001
Flavopunctelia soredica	18	1	< 0.001
Chaenotheca trichialis	15	0	< 0.001
Indicator species of the forest edge:			
Physcia stellaris	5	51	< 0.001
Melanohalea exasperatula	15	46	0.001
Lecanora albellula	9	42	< 0.001
Polycauliona candelaria	0	31	< 0.001
Physcia dubia	0	28	< 0.001
Physcia adscendens	0	18	< 0.001
Candelariella reflexa	0	15	< 0.001
Candelariella aurella	0	5	0.03

[a]Monte Carlo test with 4999 permutations.

Table 4. Indicator species for large- and small-diameter trees of *Larix sibirica*.

	Indicator values (%)[a]	P^b
DBH < 40 cm:		
Lecidella euphorea	30.0	0.04
DBH ≥ 40 cm:		
Pseudevernia furfuracea	40.3	0.008
Hypogymnia bitteri	11.1	0.02
Anaptychia ulotrichoides	8.3	0.02
DBH ≥ 50 cm:		
Polycauliona candelaria	78.8	< 0.001
Physcia dubia	45.6	< 0.001
Hypocenomyce scalaris	31.9	< 0.001
Candelariella reflexa	26.5	0.006
Flavopunctelia soredica	25.1	0.002
Physcia adscendens	19.3	0.01
Physconia enteroxantha	15.8	0.01
Physcia caesia	14.3	< 0.001
Phaeophyscia orbicularis	10.2	0.01
Lecanora impudens	9.5	0.008
Collema subflaccidum	9.5	0.01
Peltigera didactyla	9.5	0.01
Cladonia pocillum	8.7	0.02
Aspicilia cinerea	6.6	0.05

[a]Percent of perfect indication.
[b]Monte Carlo test with 4999 permutations.

Table 5. Results of the CCA analysing the effect of tree species (*Betula* vs. *Larix*), habitat (forest interior, forest edge), and stem diameter on the epiphytic lichen vegetation (63 species; total variance 3.62) on the trunks of 20 birch and 40 larch trees at Site 1.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.409	0.172	0.092
Randomised data for eigenvalue[a]	0.095	0.056	0.033
Species-environment correlations	0.924	0.822	0.583
Randomised data for correlations[a]	0.580	0.522	0.473
Interset correlations			
Tree species	−0.912	−0.014	−0.096
Habitat	−0.007	−0.815	0.078
Stem diameter (DBH)	0.374	0.213	−0.512

[a]Significant at $P = 0.001$ according to Monte Carlo permutation test with 999 iterations.

and Coxson 2002) or the improved (moderate) nutrient supply in nutrient-poor environments (Hauck et al. 2012). Eutrophication, however, is adverse to many epiphytes (Hauck 2010; Johansson et al. 2012).

In the Kazakh Altai, species with preference for the forest edge included light and nutrient-demanding lichens (Wirth 2010), such as *Polycauliona candelaria*, *Candelariella*, *Physcia*, *Phaeophyscia*, *Physicella*, *Xanthomendoza ulophyllodes* (= *Xanthoria u.*, *Oxneria u.*), *Melanohalea exasperatula*, and *Lecanora hagenii*. Species with higher abundance in the forest interior included several species of the Parmeliaceae (*Parmelia*, *Hypogymnia*, *Parmeliopsis*, *Flavopunctelia*, *Vulpicida*, *Pseudevernia*, *Bryoria*, *Usnea*) with preference for nutrient-poor to only slightly nutrient-enriched substrates, but not necessarily for shade. *Chaenotheca stemonea*, *C. trichialis*, and the rare *C. gracilenta* need nutrient-poor and shady trunk bases (Holien 1996; Hauck and Wirth 2010). The dominance of the Parmeliaceae suggests that the gradient of increasing nutrient availability from the interior to the edge is more important than the concurrent gradient in solar irradiation. The shade-adapted *Chaenotheca* species were doubtlessly promoted by the dense shrub layer in the studied forests.

Many lichens with preference for large-diameter trees were also species which are characteristic of moderately nutrient-enriched substratum. This coincidence is attributable to the fact that big larch trees often have a spreading system of coarse roots of several centimetres to few decimetres in diameter above the soil level, where nutrients can accumulate (Figure 7). Large trees are also

preferred resting places of livestock and thus their bases are exposed to the elevated deposition of nitrogen and other nutrients. Dust accumulated at the trunk bases also influences lichen distribution and is likely to account for the occurrence of the usually saxicolous *Aspicilia cinerea* and the terricolous *Cladonia pocillum* at the base of some large-diameter trees. By contrast, thin-stemmed larch trees with predominantly vertical surfaces typically have, like most other conifers, very acidic and nutrient-poor bark (Kalgutkar and Bird 1969; Hauck et al. 2012). Large-diameter trees also differ from trees with thin trunks by their higher structural diversity (in addition to the mentioned structural features of the coarse roots) and longer habitat continuity, which may facilitate the colonisation by species with limited dispersal abilities (Hilmo and Såstad 2001). In the present study, the known ecology of the species which were identified to prefer large-diameter trees (Table 4) does not suggest that dispersal limitations were a key factor linked to this specialisation.

The disturbance at the edges of the studied forest stands exceeded the level which can be beneficial for lichen species diversity (Connell 1978; Hughes 2010). This was indicated by the reduced tree-level species richness and the low N_1-diversity at the forest edge. It is plausible that the heavy disturbance in the past due to selective logging, fire and livestock grazing had an adverse effect on lichen diversity at the forest edge. However, it was not possible to test this hypothesis empirically, because undisturbed forest edges were lacking. The scarcity of many species under the edge conditions (among others the Parmeliaceae species with often relatively large foliose or fruticose thalli) allows other species (sometimes species with low frequency; Figure 8) to become more dominant in the edge vegetation than in the forest interior. These include nitrophytes, such as *Massjukiella*, *Physcia*, *Phaeophyscia*, and *Physconia*. The reduced tree-level species richness indicates that the increase of nitrophytic species cannot compensate for the reduced diversity of forest species. Replacement of larch by birch after heavy disturbance only introduced a few characteristic species (e.g. *Arthopyrenia punctiformis*) into the ecosystem. However, data for birch was from a single site which allows preliminary conclusions only.

The species richness of larch-inhabiting epiphytic lichens was only partly higher in the forest-steppe ecotone of the Kazakh than the Mongolian Altai (Hauck et al. 2012). The total species richness at the landscape level

Table 6. Species with significant preference for birch (data from Site 1).

	Frequency (%)[a]			Cover (%)		
	Birch	Larch	P[b]	Birch	Larch	P[b]
Arthopyrenia punctiformis	90 ± 7	−	< 0.001	2.0 ± 0.6	−	< 0.001
Melanohalea exasperata	55 ± 5	−	< 0.001	2.1 ± 0.7	0.0 ± 0.0	< 0.001
Athallia pyracea	10 ± 7	−	0.03	0.1 ± 0.0	−	0.02
Candelariella aurella	10 ± 7	−	0.03	0.0 ± 0.0	−	0.02
Hypogymnia tubulosa	20 ± 10	5 ± 3	0.05	0.2 ± 0.1	0.0 ± 0.0	0.03

[a]Frequency on sample trees of birch ($N = 20$) and larch ($N = 40$).
[b]U-test.

Figure 7.   Old larch tree with extensive coarse-root system above the ground at the forest edge in the Kazakh Altai. Such trees are hotspots for epiphytic lichen diversity in the Central Asian forest-steppe.
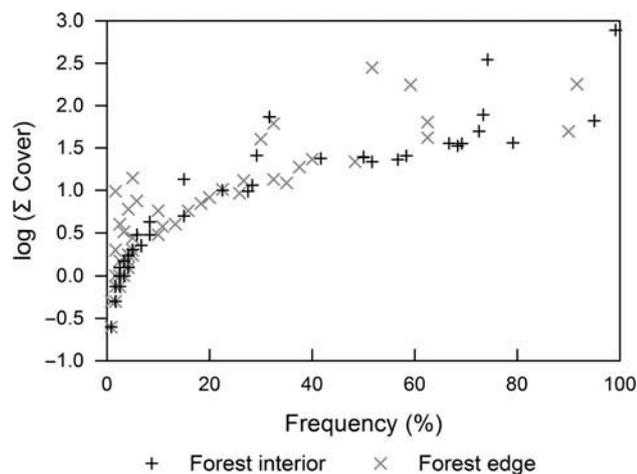

Figure 8.   Logarithmic sum of cover (in % of the available trunk area from 0–1 m above the soil surface) versus frequency (in % of sample trees) of the individual lichen species ($N = 87$) growing in the forest interior or at the forest edge.

(γ-diversity) in the Kazakh Altai (87 species) exceeded that in the Mongolian Altai (64 species). Tree-level α-diversity (Kazakhstan: 12.6 ± 0.8 species tree^{-1}; Mongolia: 12.0 ± 2.3 species tree^{-1}) and plot-level α-diversity (Kazakhstan: 31.3 ± 2.6 species plot^{-1}; Mongolia: 29.0 ± 0.7 species plot^{-1}) in forest interior plots did not differ between the Kazakh and the Mongolian Altai. This suggests that an equal number of species is adapted to the rather different climatic conditions in the larch-dominated forest-steppe of the eastern Eurosiberian and western Chinese–Mongolian steppe regions. The differences in species richness at the landscape level are caused by differences occurring in the α-diversity at the forest edge at both the tree level (Kazakhstan: 9.4 ± 0.4 species tree^{-1}; Mongolia:

5.6 ± 2.5 species tree^{-1}) and the plot level (Kazakhstan: 35.2 ± 3.6 species plot^{-1}; Mongolia: 21.8 ± 4.7 species plot^{-1}). The lower species richness at the forest edge in the Mongolian Altai may partly be due to the more arid and harsher climate at 2300–2400 m a.s.l. on the leeward side of the Altai mountain range. These climatic conditions could limit the species diversity, for example, by wind and snow abrasion (Esseen and Renhorn 1998). However, the lower species diversity is likely to be also due to the considerably higher livestock density in the Mongolian than the Kazakh Altai (Hauck et al. 2012; Lkhagvadorj et al. 2013).

Conclusions

Larch trees in the strongly degraded forest edges of the forest-steppe of the Kazakh Altai are less diverse in epiphytic lichens and harbour fewer specialist species than trees in the forest interior. Over-intense forest use for selective logging and livestock grazing and the effect of fire in the past could be a plausible explanation of the comparably low lichen diversity at the forest edges. While the low species diversity at the forest edges is supportive of the first hypothesis, the second hypothesis – that the milder climate of the less highly elevated, warmer and more humid Kazakh Altai causes a higher species richness of epiphytic lichens than in the Mongolian Altai – is not clearly supported by the data. Rather, it is likely that the observed differences in the total species richness are caused by different disturbance regimes at the forest edges. The results of the present study suggest that the reduction of anthropogenic disturbance at the forest edges and the conservation of large-diameter trees are needed to protect the epiphytic lichen richness of the forest-steppe of the Kazakh Altai.

Acknowledgements

Notes on contributor

Markus Hauck is Professor; his research interests include the biodiversity and ecosystem functions of forest and grassland ecosystems in the boreal and temperate zones.

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