

Edge and land-use effects on epiphytic lichen diversity in the forest-steppe ecotone of the Mongolian Altai

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Abstract

Epiphytic lichen diversity was studied in forests of Siberian larch (*Larix sibirica*) in the forest-steppe ecotone of the Mongolian Altai. These forests are utilized for livestock grazing, fuelwood collection and occasional logging by pastoral nomads. The density of nomad households in the proximity of the forests influences epiphytic lichen diversity more strongly than the position of sample trees in the forest interior or at the forest line to the steppe. This suggests that land use exerts a stronger effect on lichen diversity than the distinct gradient in microclimate between the forest interior and the forest edge. The co-occurrence of nitrophytes with anitrophytic acidophytes on a small spatial scale as well as higher N and Ca concentrations and pH values in the bark of larch trees at the forest edge than in the forest interior indicate that moderate livestock grazing increases the epiphytic lichen diversity due to an increase of the diversity of chemically different microhabitats. Preferences of many lichen species (and of rare species in particular) for overmature and decaying trees suggests that logging and fuelwood collection has adverse effects on epiphytic lichen diversity. This adverse effect is likely to be more crucial for lichen diversity than the putatively positive effect of livestock grazing, since more lichens with a preference for old and decaying trees than for nitrogen-enriched bark were found. The present study is the first one investigating the impact of pastoral nomadism in Central Asia on epiphyte diversity.

Keywords: Lichen-forming fungi, Pastoral nomadism, *Larix sibirica*, Livestock grazing, Logging, Fuelwood collection

Introduction

Forests in Central Asia's forest-steppe ecotones are highly fragmented. The occurrence of the forests in patches can generally have natural causes, as forests are limited to the sites with the best water availability, in mountainous regions usually to the north-facing slopes (Dulamsuren et al., 2009), whereas dry sites are covered by grasslands. Forest fragmentation exerts well documented effects on epiphytic lichens by changes in microclimate. Forest edges are generally characterized by higher values and higher variability of solar irradiation, temperature and humidity than the forest interior (Davies-Colley et al., 2000; Heitkecker and Halpern, 2007). This influences lichen abundance, species composition and growth rates of epiphytes (Sillett, 1994; Rheault et al., 2003). Furthermore, epiphytes at the forest edge are affected by higher wind speeds, which result in more pronounced wind and snow abrasion (Esseen and Renhorn, 1998; Hilmo and Holien, 2002). In general, edge effects are more significant under dry than moist conditions, as differences in microclimate between edge and interior become more effective with increasing aridity (Kivistö and Kuusinen, 2000). Forest-steppe borders in Central Asia are dry environments, where precipitation is just sufficient for tree growth (Gunin et al., 1999; Dulamsuren and Hauck, 2008). In an ungrazed forest-steppe ecotone of northern Mongolia, epiphytic lichen vegetation was found to be strongly reduced in terms of species diversity and cover at the sun-exposed forest edge compared to the interior of larch dominated taiga forests (Hauck et al., 2007). However, at many places of Central Asia the climate-dependent forest edge-interior gradient is disturbed by the influence of human land use.

Humans have reduced the forest area and fragmented the remaining stands by logging, livestock breeding and fire (Hilbig, 1995; Kaiser et al., 2009). The Altai Mountains belong to the oldest settlement areas in Central Asia; modern humans are thought to have appeared there between 100,000 and 60,000 years ago (Rybin, 2005; Schlütz and Lehmkuhl, 2007). Thus, vegetation has been subject to human land use since millennia. People in this region are thought to have started to make their living as pastoral nomads between 2000 and 3000 years ago (Novgorodova, 1989; Rudaya et al., 2008), a subsistence strategy that is pursued by most of the population until today. This lifestyle includes housing in traditional nomad tents (gers)

and an extensive system of livestock breeding where different kinds of animals search appropriate pastures throughout the year by themselves without or with only little additional feeding even during winter (Bazargur, 2002; Janzen, 2005). The livestock primarily grazes in the steppe, but also forest margins and less intensively the interior of forests are utilized for pasture (Tsogtbaatar, 2004; Sankey, 2006). Mixed stocks of goat, sheep, cattle, yak, horses and camels are common. Recently, the grazing pressure on the forests is supposed to be growing, as the number of goats increased due to a higher demand for cashmere wool from the Chinese and Mongolian markets (Lecraw et al., 2005). Deadwood, including branches of living trees, is legally collected as fuel wood, while living trees are (often illegally) felled to harvest construction wood for sale (Erdenechuluun, 2006). The local land-use pressure on forests varies with the proximity to the next nomad dwelling (Okayasu et al., 2007). This applies especially to the grazing pressure and to the collection of fuel wood, whereas construction wood is harvested in different distances from the gers depending on the availability of good timber and compliance with law.

Effects of the location of trees within the forest-steppe ecotone or land-use intensity on epiphyte diversity have rarely been studied in Central Asia (Hauck et al., 2007), even though a crucial role of these factors is to be expected, because epiphytes respond to microclimate (Baldwin and Bradfield, 2005; Belinchón et al., 2007), nitrogen availability (van Herk, 1999), mechanical damage by livestock (Fuertes et al., 1996), and the availability of deadwood (Humphrey et al., 2002; Bunnell et al., 2008). Since lichens are the most important group of epiphytes in the continental mountain climate of the Altai Mountains, we studied edge and land-use effects on epiphytic lichen diversity in monospecific forests of Siberian larch (*Larix sibirica* Ledeb.), Mongolia's most common forest ecosystem (Tsogtbaatar, 2004). While edge effects were systematically studied by selecting pairs of sample plots inside the forest and at the forest line to the steppe, the spatial variation of land-use intensity was included as a covariate, after the plots had been selected according to other criteria, notably minimum size of the forest stand, approximate equidistance between the stands and geomorphological features.

The objective of the study was to test the hypotheses that (1) lichen species diversity is reduced at the forest line to the steppe compared to the forest interior, (2) the dominance of nitrogen-tolerant species in epiphytic lichen vegetation is higher at the forest line than in the forest interior, and (3) livestock grazing, logging and deadwood collection as firewood reduce

epiphytic lichen diversity. To test these hypotheses, epiphytic lichen diversity of 240 tree trunks was studied in total. The consequences of firewood collection were assessed by comparing the lichen diversity on coarse deadwood with that of living trees to test the hypothesis (4) that certain lichen species are predominately or exclusively occurring on decaying logs. Aside from testing these specific hypotheses, the study also aims at increasing the knowledge of the lichen vegetation of western Mongolia, as this region has been very little studied, so far (Cogt, 1995).

Material and methods

Study area

Field work was carried out in the Mongolian Altai in the Altai Tavan Bogd National Park in the province ("aimag") of Bayan-Ulgii, western Mongolia, 110 km SW of the city of Ulgii. Vegetation of the study area is dominated by alpine meadows, relatively moist true steppe and dry mountain steppe. Forests occur on north-facing slopes between an elevation of ca. 2000 and 2500 m a.s.l. in contact to true steppes and alpine meadows. Forests usually grow only on the upper, or if an alpine treeline is present, the central parts of the mountain slopes. The lack of forests on the slope base can be assumed to be the result of the long-standing human influence in the Altai Mountains. Individual trees or small forest stands in the valley of the Khovd River, which is the main stream in the Mongolian Altai, suggest the former occurrence of more extended forests in river valleys. The flanks of the central chain of high peaks of the Mongolian Altai (up to 4734 m a.s.l.) are also covered by forests at their base. Most forests are only formed by Siberian larch, whereas Siberian spruce (*Picea obovata* Ledeb.) and Siberian cedar (*Pinus sibirica* Du Tour) rarely contribute to the forest assemblages at the foot of the high peaks.

The density of climate data available from the Mongolian Altai does not appropriately reflect the spatial climatic variability that has to be expected given the variation of altitude, relief and vegetation. Annual precipitation in the study area is roughly assessed to amount to 250 to 300 mm at 2000 m a.s.l. (Rudaya et al., 2008) with a clear peak in summer. Mean July temperatures are in the range of 12 to 15 °C, whereas January temperatures are estimated to

be around -24 to -25 °C (Rudaya et al., 2008). Geologically the Mongolian Altai is dominated by siliceous rock, including granite and schist. The prevailing forest soils are Leptosols.

Sample plots

Field work was carried out in July 2010. Six forested sites were selected on the northern flank of a mountain ridge located 2 to 7 km S and SSE of Lake Dayan Nuur (48°23' N, 88°55' E). The geographical position, elevation and aspect of these sites are compiled in Table 1. The distance between neighboring sites amounted to 2.2±0.5 km. Site selection was a non-random procedure, but included all available forest islands on the studied mountain range; thus the selection procedure largely excluded the subjective choice of sites. Relatively moist depressions, which occur locally on the mountain slopes were deliberately avoided to improve the comparability between the sites. At each site, two plots each of 20 m × 20 m size were selected. One of them was located at the forest edge with lower boundary of the plot being identical with the forest line to the steppe. The other one was located at least 50 m within the forest interior.

The forest edge of the larch forests of the Mongolian forest-steppe is generally more sun-exposed, warmer and drier than the forest interior (Dulamsuren et al., 2009), but measurements from the study plots are unavailable. Forests of the Mongolian Altai are mostly open and sun-exposed. The canopy closure rarely exceeds 40 % (Table 1). Nevertheless, stand densities are highly variable, but this is primarily due to differences in the abundance of small trees from regeneration after disturbances. Higher stand densities at the forest edge than in the interior (Table 1) increased regeneration after logging, which is more intense in the forest edge than the interior, but do usually not result in higher canopy density (Table 1).

Recording the lichen data

Epiphytic lichen vegetation was studied on 20 trees per plot with a dbh of ≥15 cm. If more than 20 trees per plot met this criterion, the 20 trees growing most closely to the lower edge of the plot were selected. On plots where less than 20 trees with a dbh ≥15 cm were available, the relevant number of trees growing most closely to the sample plot was selected in addition

to the trees on the plot. The number of studied trees growing outside the plots is specified in Table 1. This procedure of sample tree selection was employed, even though most 20 m × 20 m plots harbored less than 20 trees with a dbh ≥15 cm, because the plots were selected with the aim to study the diversity of various other plant and animal groups as well.

On each sample tree, all individual lichen species were recorded on the trunks in a height of 0 to 1 m above the ground, including all aspects, i.e. the whole circumference of the trunk. The cover of each species was estimated in percent. These estimations are facilitated by the fact that 1 % equals 1 cm of the whole stem circumference covered by the relevant lichen. Cover values of <1 % were processed with the value of 0.5 % in the data analyses. The recording of lichens was limited to the lowest 1 m of the tree trunks, because the stems were virtually avoid of lichens above this height. The present study thereby differs from former analyses of the epiphytic lichen diversity in coniferous forests by our group inside (Hauck et al., 2007; Hauck and Javkhlan, 2009) and outside (e.g. Hauck and Spribille, 2005) Mongolia where cover values refer to the lowest 2 m of the trunk surface. Field work was carried out in July 2010. Nomenclature is based on Wirth et al. (2011) and for the only taxon not included therein (*Physconia hokkaidensis*) on Chen and Hu (2005). Thin-layer chromatography was applied for the identification of lichen secondary compounds where appropriate for species identification.

At one site (site 5), 10 dead, mostly decorticated tree trunks, lying on the forest floor, with a diameter between 27 and 45 cm (35±2 cm) were studied in addition to the living trees. At most other sites, coarse deadwood abundance was too low for a comparative study. Even at site 5, the density of deadwood on the 20 m × 20 m forest-interior plot was so low that sampling had to be extended to a radius of 300 m around the plot; at the forest edge, coarse deadwood was virtually lacking. On the dead tree trunks, the presence of lichen species was qualitatively recorded. Cover values were not estimated, as the size and shape of deadwood are more variable than that of living trees and thereby reduce the comparability between the individual pieces of deadwood. The data of the dead trees are compared with the forest-interior plot of the same site with 20 trees with a mean diameter of 34±2 cm (range from 15 to 49 cm).

Estimation of land-use intensity

All sample plots were subject to occasional logging. The diameter at breast height (dbh) distribution of sample trees (Fig. 1) deviates from the reversed J-shaped distribution, which is characteristic of most unmanaged forests (McCarthy and Weetman, 2006). Trees with high dbh were very rare on the sample plots (Fig. 1; Table 1); unfilled dbh classes, especially at a dbh of ≥ 50 cm, but also at lower dbh indicate that the natural age structure is heavily disturbed. The higher proportion of thin trees at the forest edge than in the forest interior gives evidence of more pronounced logging in the proximity to the steppe than in the interior of the forest.

The individual sites differed in land-use intensity despite their proximity. For a rough assessment of land-use intensity, four parameters were recorded: (1) the number of pastoral nomad families having their summer camps in a radius of 1 km around the individual study sites (calculated from the forest edge plot), (2) the above-ground biomass of the herbal layer and (3) the density of livestock dung as a proxy for grazing intensity, (4) the total of tree stumps divided by the total of living trees per plot with a dbh ≥ 5 cm. The number of nomad families in the neighborhood of the study sites was determined by recording the geographical coordinates of all gers in the valley in front of the studied mountain range. For assessing the biomass of the herbal layer, the complete above-ground biomass was harvested in five randomly selected 1 m \times 1 m subplots per plot. The dry weight was determined after drying the pre-dried samples for 24 h at 105 °C. This was done without temporal replication, as all samples were taken within 2 weeks. Data assessing the land-use intensity at the individual sites are included in Table 1.

Bark chemistry

Bark was sampled as a bulk sample from all aspects of each sample tree at the lowest 1 m of the trunk. Epiphytes were carefully removed from the bark surface with a pocket knife during sampling. Bark samples were dried at 105 °C and homogenized in a swing mill using an insert that is free from metal abrasion. The bark powder was used to determine the C and N concentrations using a C/N analyzer (Vario EL III, Elementar Analysensysteme, Hanau, Germany). Bark pH was measured with an MP 120 pH meter with electrode InLab 413

(Mettler-Toledo, Greifensee, Switzerland) in suspensions with deionized water (25 ml per g dry weight) shaken for 24 h before the measurements (pH [H₂O]); afterwards KCl was added in an excess concentration to measure the pH (KCl) value. After acid digestion with 65 % HNO₃, the total concentrations of K, Na, Ca, Mg, Fe, Al, Mn, Zn, Cu, P, and S were analyzed with ICP-OES using an Optima 5300DV (Perkin Elmer, Waltham, Massachusetts, USA).

Statistics

Arithmetic means \pm standard error are presented throughout the paper. All data were tested for normal distribution with the Shapiro-Wilk test. Significance of differences in the bark chemistry data, which were normally distributed, was tested with Student's *t*-test. Frequencies of lichen species on different collectives of sample trees was tested for significant differences with the χ^2 -test. These analyses were calculated with SAS 6.04 software (SAS Institute Inc., Cary, North Carolina, USA). Detrended correspondence analysis (DCA) was applied to study differences between different tree collectives in variation of epiphytic lichen abundance with the program PC-Ord 5.14 (MjM Software, Gleneden Beach, Oregon, USA). The length of the gradients along the ordination axes are given in SD and represent the average standard deviation of species turnover.

Results

Epiphytic lichen diversity on living trees

A total of 64 lichen species was found on the 240 studied larch trees. The forest interior accommodates more lichen species than the plots at the forest edge to the steppe. The total of lichen species per sample tree varied between 7.5 and 13.1 on the forest interior plots, but between 2.4 and 12.6 on the plots at the forest edge (Fig. 2a). The plot-wise means amounted to 12.0 ± 2.3 lichen species per tree in the forest interior and 5.6 ± 2.5 species per tree at the forest edge. Most tree trunks had a sparse lichen cover. Every 10th tree at the forest edge was not inhabited by any lichen (13 trees; 10.8 %). Though this statement refers only to the sampling height of the lowest 1 m of the trunk, in most cases these trees were completely devoid of lichens at any height visible from the ground. In the forest interior, most larch

trunks were colonized by lichens; only on one tree, no lichens were observed at the sampling height. The mean cover of lichens was higher in the forest interior (12.0 ± 2.3 %) than at the forest edge (5.6 ± 2.0 %) (Fig. 2b).

Despite the strong differences in species richness and cover between the forest interior and the forest edge, trees of these two habitats were not clearly separated from one another in the ordination analysis (DCA; Fig. 3). Nevertheless, most trees from the forest interior had low scores along axis 1, whereas trees from the forest edge dominated at high axis 1 scores. Trees with low axis 1 scores showed little variation along axis 2; at axis 1 scores < 1.5 , the length of the gradient along axis 2 varied between 0.5 and 1.5 SD. At high axis 1 scores, the gradient length along axis 2 rose to 4.5 SD and exceeded thereby the total gradient length along axis 1 (3.9 SD).

Only a few species, including *Lecanora varia* (occurring on 40 % of the sample trees) and *Vulpicida pinastri* (on two-thirds of the trees), were more or less evenly distributed over the ordination space in the DCA (Table 2). Excluding rare species which occurred on less than 5 % of the sample trees, 15 lichen species were preferably found on trees with low axis 1 scores (usually < 2 SD). Examples of such species include *Hypogymnia bitteri* (Fig. 4a), *Parmelia sulcata* (Fig. 4b), *Bryoria fuscescens*, and *Parmeliopsis ambigua* (group A in Table 2). In addition, 14 rare species, which occurred on less than 5 % of the sample trees, were observed on the trees with low axis 1 scores (Table 3). *Xanthoria candelaria* (Fig. 4f), *Physcia dubia* (Fig. 4g), *Lecanora hagenii* (group B in Table 2) and 16 rare species are characteristic of trees with high axis 1 (> 2 SD), but low axis 2 scores (< 2.5 SD; Table 3). A group of six frequent (≥ 5 % of sample trees) and three rare (< 5 % of sample trees) species was found on trees of both groups A and B (Table 2, 3). Examples include *Amandinea punctata* (Fig. 4c), *Cladonia pyxidata* s.l. (Fig. 4d), *Melanelixia fuliginosa*, and (with a preference for group B) *Candelariella reflexa* (Fig. 4e). Only two species, *Arthonia apatetica* (Fig. 4h) and *Lecanora albellula* (Fig. 4i), were preferably found on trees with high axis 1 scores ($> [1-]2$ SD) and high axis 2 scores ($[1-]2-4$ SD; group C in Table 2).

Species diversity increased with increasing tree diameter (Fig. 5). Six lichen species were only found on trees with a dbh ≥ 50 cm (*Heterodermia speciosa*, *Lecanora allophana*, *Leptogium tenuissimum*, *Peltigera didactyla*, *P. rufescens*, *Placynthiella dasaea*) and seven further species were restricted to trees with a dbh ≥ 40 cm (*Bacidia circumspecta*,

Candelariella xanthostigma, *Cladonia bacilliformis*, *Lecanora chlarotera*, *L. hypoptoides*, *Megaspora verrucosa*, *Physciella chloantha*). All these species grew at the trunk base and especially on coarse roots very close to the soil surface, often in microhabitats where the bark was partly sheltered from the sun by grasses and herbs.

Both the number of lichen species and the total mean cover of all lichen species per tree decreased with human population density in the neighborhood (Fig. 2). At the forest edge to the steppe, significant negative correlations were found for lichen diversity and cover with the total of summer camps of pastoral nomad families located within a radius of 1 km from the forest edge plot. Similar trends are observable in the forest interior, but the correlations are not statistically significant and the slopes of the regression lines are less steep than at the forest edge. Significant correlations with other parameters describing land-use intensity, including herbal above-ground biomass, livestock dung density or tree stump density were not found (results not shown).

Lichens on deadwood

The ten dead, lying, often largely decorticated larch trunks, which could be studied in and around the forest-interior plot of site 5 were inhabited by 35 lichen species. Sixteen of them were significantly more frequent on the deadwood than on the living larch trees of the same plot, whereas only six species occurred more frequently on the trunks of living trees than on deadwood (Table 5). In the case of 25 species, the χ^2 test does not yield a significant result, as these species either have no preference for living or dead trees or are too rare to get a significant test result irrespective of their ecological preferences. *Buellia griseovirens*, *Candelariella vitellina*, *Xylographa parallela*, *Ochrolechia szatalaënsis* and *Physia stellaris* were only found on coarse deadwood during the present study.

Bark chemistry

Larch bark at the forest edge was less acidic and contained significantly more N and Ca than bark from the forest interior (Table 4).

Discussion

Epiphytic lichen diversity in the forest-steppe ecotone of the Mongolian Altai is clearly influenced by land use connected to the traditional pastoral livestock husbandry. Nomad families living in grasslands close to the forest affect lichen diversity through livestock grazing and the harvest of firewood and construction wood. The anthropo-zoogenic impact on epiphytic lichen vegetation varies between individual forest stands and depends on the density of nomad households having their summer camp in the neighborhood of the forest. This influence is for obvious reasons more pronounced at the forest edge to the steppe than in the forest interior. However, proximity to nomad gers (Fig. 2) is more crucial for the variation of epiphytic lichen abundance than the location of trees at the forest edge or in the forest interior, as can be inferred from ordination analysis (Fig. 3). Thus, in dependence on the population densities of humans and livestock in the steppe, the anthropo-zoogenic disturbance effect reaches over varying distances into the forest. At low human population density near the forest, there is a fast species turnover along the gradient from the forest edge to the forest interior. These differences in species composition between forest edge and interior are primarily caused by differences in microclimate and were found to be relatively sharp in the ecotone between a *Larix sibirica* forest and the steppe in an area of northern Mongolia (Khentey Mountains), which is traditionally not inhabited by pastoral nomads (Hauck et al. 2007). Like in the Mongolian Altai, *Lecanora albellula* (= *L. piniperda*) was among the dominant species at the forest edge in the Khentey Mountains. Pronounced microclimate-driven influences on the epiphytic lichen vegetation were also observed in xeric Mediterranean oak forests (Belinchón et al., 2007) and in south-facing edges of spruce forests in northern coniferous forests of Scandinavia (Kivistö and Kuusinen, 2000).

The poor delimitation of forest-interior and forest-edge trees in the DCA ordination (Fig. 3) highlights the severity of the anthropo-zoogenic impact on the larch forests in the Mongolian Altai, as this influence is capable of leveling the effects of the strong microclimatic gradient in the forest-steppe ecotone. Our data suggest that (1) the logging of old trees, (2) the removal of deadwood and (3) the nutrient enrichment by livestock grazing affect epiphytic lichen diversity. The increase of lichen diversity with tree diameter (Fig. 5) and the preference of many rare species for thick trees emphasize their significance for maintaining lichen diversity. The importance of old trees for lichens due to the availability of a much higher variety of

microhabitats than on younger trees has been shown repeatedly (Johansson et al., 2007; Nascimbene et al., 2009). Moreover, the habitat continuity ensured by old trees is essential for epiphytes with low dispersal abilities (Hilmo and S astad, 2001). Old trees with a diameter >40 cm were rare in the studied forests, which is doubtlessly attributable to logging as can be inferred from the high number of tree stumps at the study sites (Table 1). This implies that logging may have considerably reduced the diversity of epiphytic lichens in the Mongolian Altai.

Similarly as with the old trees, several lichen species are more abundant on or even limited to coarse deadwood. The significance of deadwood for lichen diversity is also well studied in other regions (Bunnell et al., 2008). The customs to collect deadwood as fuel, which is preferential in order to sustain the forested area and is forced by law, has thus the disadvantage that the lichen diversity of the forest ecosystem is reduced due to the loss of deadwood-inhabiting species. Some lichen species (e.g. *Lecanora hypoptoides*, *Megaspora verrucosa*) likewise prefer deadwood and thick living trees. However, as the density of thick trees is as dramatically reduced as the density of deadwood, this ecological flexibility does not lead to a lower threat of the relevant species in the Mongolian Altai.

Livestock grazing reduces the biomass of the ground vegetation, which most likely is of subordinate significance for lichen diversity. However, since some lichens are limited to shaded bark areas at the trunk base and on roots immediately above the soil at the forest edge, constant removal of tall grasses and herbs by livestock could have slightly reduced lichen diversity. Mechanical damage through browsing animals certainly destroys individual lichen thalli, but it is not probable to assume that this reduces the lichen diversity on the stand or landscape level under the given livestock densities in the Mongolian Altai. However, a strong effect is apparently exerted through the enrichment of the tree bark and wood with nutrients. The higher concentration of N in the larch bark from the forest edge than the forest interior is attributable to the nutrient input by livestock, as other sources are lacking. The higher Ca content as well as the lower acidity of bark at the forest edge might be due to a combined effect of the deposition of particulate matter from the steppe and the input by livestock.

Epiphytic lichen vegetation responds very sensitively through changes in the species composition to already minor changes in substratum pH and nutrient availability (Gauslaa et al., 1998; Hauck et al., 2011). Several species found during the present study, including

Xanthoria candelaria, *Physcia dubia*, *Amandinea punctata* and *Candelariella reflexa*, are nitrophytes (van Dobben and de Bakker, 1996). Their occurrence in the larch forests of the Mongolian Altai surely depends on livestock grazing. Conifer bark is generally too acidic and too poor in nutrients for these species (Gauslaa and Holien, 1998; van Herk, 2001; Hauck and Spribille, 2005). In the Mongolian Altai, nitrophytic species occurred in close spatial relationship with acidophytic species, which are typical of not nutrient-enriched conifer bark, and with species requiring mineral-rich, but only slightly nitrogen-enriched bark (e.g. *Bacidia circumspecta*, *Megaspora verrucosa*). This small-scale pattern of lichens with different nutrient requirements confirms the absence of significant atmospheric nitrogen deposition, as otherwise a more even distribution of nitrophytes in the forests or at least along the forest edges would have to be expected (van Herk et al., 2003). Furthermore, this spatially heterogeneous pattern suggests that (moderate) livestock grazing increases the epiphytic lichen diversity in the forest-steppe ecotone of the Mongolian Altai, as it increases the variety of microhabitats with different nutrient concentrations and pH conditions. Nutrient and tree-diameter effects are interrelated, because nutrient-enriched bark is primarily found on large trees, which are preferably haunted by livestock in search of shade and also offer a higher quantity of horizontal bark surfaces at the trunk base where nutrients can accumulate. Therefore, lichen species preferring old trees and nutrient bark at sun-exposed sites form a common group in the ordination space (group B in Tables 2, 3). Young trees provide only small horizontal bark areas and are not favored by livestock and are thus inhabited by different lichens (group C in Table 2, 3). These diverse site conditions at the forest edge and in heavily grazed areas of the forest interior are likely to cause the higher gradient length (i.e. higher species turnover) along axis 2 than axis 1 of the DCA in Fig. 3.

Conclusions

Land-use by pastoral nomads in the forest-steppe ecotone of the Mongolian Altai clearly affects epiphytic lichen diversity. Livestock grazing in the forest seems to increase epiphytic lichen diversity at the present grazing pressure by locally creating nutrient-enriched microhabitats on the otherwise acidic and nutrient-poor bark surface of the larch trees. By contrast, logging and the collection of deadwood are strongly detrimental for epiphytic lichen diversity. The observation of many rare species on single overmature trees and decaying tree boles suggests that logging and firewood collection might have increased recently. If the number of overmature and decaying trees was as low as today already during the last 2000 or

3000 years when pastoral nomads settled in the Mongolian Altai, then it would be likely that species diversity would be much more reduced. Today, several lichen species occur only with single thalli on single old trees or deadwood pieces in the forests. These species are probably threatened not only by the removal of the inhabited trees and wood by humans, but also intrinsically by the small size of their populations itself, which might limit the capacity for reproduction and dispersal. The high number of overmature and decaying trees and the relatively low number of nitrophytic species suggests that the negative land-use effects strongly dominate over the positive ones. To our knowledge, the present study is the first one substantiating a loss of epiphyte diversity by pastoral nomadism in the Eurasian steppe belt.

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Table 1.

Location of study sites and measure of land-use pressure

	Hab. ^a	Site					
		1	2	3	4	5	6
Latitude (N) ^b		48°14'39"	48°15'16"	48°15'35"	48°16'3"	48°15'12"	48°14'59"
Longitude (E) ^b		88°57'0"	88°54'25"	88°54'11"	88°51'35"	88°50'17"	88°55'57"
Altitude (m a.s.l.) ^b		2375	2335	2300	2320	2375	2305
Gers in a radius of 1 km ^c		15	6	14	1	4	3
Herbal phytomass (g m ⁻²) ^c	FI	43±6	58±8	79±9	33±5	71±16	59±7
	FE	28±4	66±6	60±7	48±7	92±16	87±22
Dung abundance (ha ⁻¹)	FI	580	155	60	60	30	70
	FE	465	265	210	70	160	240
Canopy closure (%)	FI	40	40	35	40	40	40
	FE	40	40	30	50	40	40
Tree stumps (ha ⁻¹) ^d	FI	1700	1150	2050	2175	2150	3250
	FE	1600	2000	1225	2125	1925	900
Stand density (trees ha ⁻¹) ^e	FI	1200	525	975	600	1000	1400
	FE	1850	4225	1625	1025	1350	1075
Ratio stumps : living trees	FI	0.7	0.5	0.5	0.3	0.5	0.4
	FE	1.2	2.1	1.3	0.5	0.7	1.2
Trees with dbh _≥ 40 cm	FI	2	0	6	5	4	12
	FE	1	0	0	13	4	1
Trees with dbh _≥ 40 cm	FI	1	0	0	0	0	2
	FE	1	0	0	5	1	1
Trees outside plot included in epiphyte recording ^f	FI	7	6	11	9	9	13
	FE	2	0	0	11	6	0

^a Hab., Habitat: FE, forest edge; FI, forest interior^b Specifications refer to the sample plot at the forest edge^b 1-km radius refers to the sample plot at the forest edge^c Above-ground biomass of the herbal layer^d Not separated between felled and broken-off trees^e Trees with a dbh \geq 5 cm^f Relevant if <20 trees with a dbh \geq 15 cm were available within the 20 m \times 20 m plot (see Methods)

Table 2

Frequency of lichen species (only species which occur on at least 5% of the sample trees) on percent of the trunks (0 to 1 m above the soil level) of sample trees ($N=240$), mean cover and DCA scores indicating different ecological preferences.

Species	Freq. (%)	Mean cover (%)	DCA scores ^a		
			A	B	C
1. Preference for A:					
<i>Usnea spec.</i>	65	0.40±0.05	+	.	.
<i>Parmeliopsis ambigua</i>	63	1.75±0.25	+	.	.
<i>Bryoria fuscescens</i>	45	0.31±0.04	+	.	.
<i>Parmelia sulcata</i>	40	0.44±0.07	+	.	.
<i>Trapeliopsis flexuosa</i>	35	0.46±0.09	+	.	.
<i>Lecanora cadubriae</i>	32	0.34±0.07	+	.	.
<i>Hypocenomyce scalaris</i>	27	0.48±0.13	+	.	.
<i>Hypogymnia bitteri</i>	24	0.43±0.11	+	.	.
<i>Cladonia fimbriata</i>	20	0.11±0.01	+	.	.
<i>Calicium viride</i>	9	0.05±0.01	+	.	.
<i>Hypogymnia physodes</i>	9	0.07±0.02	+	.	.
<i>Ochrolechia microstictioides</i>	8	0.08±0.03	+	.	.
<i>Cyphelium karelicum</i>	6	0.03±0.01	+	.	.
<i>Lepraria jackii</i>	6	0.03±0.01	+	.	.
<i>Cladonia coniocraea</i>	5	0.03±0.01	+	.	.
2. Preference for A and B:					
<i>Cyphelium tigillare</i>	5	0.05±0.02	+	(+)	.
<i>Melanelixia exasperatula</i>	58	0.99±0.21	+	+	.
<i>Amandinea punctata</i>	31	0.17±0.02	+	+	.
<i>Cladonia pyxidata</i>	10	0.05±0.01	+	+	.
<i>Rinodina siphodes</i>	8	0.04±0.01	+	+	.
<i>Candelariella reflexa</i>	12	0.10±0.03	(+)	+	.
3. Preference for B:					
<i>Xanthoria candelaria</i>	66	0.97±0.17	.	+	.
<i>Physcia dubia</i>	15	0.13±0.04	.	+	.
<i>Lecanora hagenii</i>	5	0.03±0.06	(+)	+	(+)
4. Preference for C:					
<i>Lecanora albellula</i>	22	0.19±0.04	.	.	+
<i>Arthonia apatetica</i>	12	0.08±0.02	.	.	+
5. No preference:					
<i>Vulpicida pinastri</i>	66	0.48±0.05	+	+	+
<i>Lecanora varia</i>	41	0.23±0.02	+	+	(+)

^a A, low scores along axis 1 (<2 SD): mesic microclimate, half-shaded, trees of various ages; B, high scores along axis 1 (>2 SD), low scores along axis 2 (<2.5 SD): xeric microclimate, light-flooded, trees of various ages including old trees with large trunk bases and protruding coarse roots offering nutrient-enriched bark on the upper side and moist, semi-shaded bark laterally and at the lower side; C, high scores along axis 1 (>[1-]2 SD), high scores along axis 2 ([1-]2-4 SD): xeric microclimate, light-flooded, only young to middle-aged trees lacking a structurally diverse trunk base

Table 3

Frequency of rare lichen species (occurring on <5% of the sample trees) on percent of the trunks (0 to 1 m above the soil level) of sample trees (N=240). Grouping after DCA scores is the same as in Table 2.

1. Preference for A (14 species):

Arthonia mediella (0.8), *Bacidia* spec. (0.4), *Bryoria fremontii* (0.4), *Cladonia bacilliformis* (0.4), *C. pleurota* (0.4), *Evernia mesomorpha* (2.1), *Hypogymnia tubulosa* (0.4), *Lecania naegelii* (0.4), *Lecanora hypoptoides* (0.4), *L. subintricata* (4.2), *Lecidea nylanderii* (1.3), *Ochrolechia androgyna* (0.4), *Pseudevernia furfuracea* (1.3), *Trapeliopsis granulosa* (0.8)

2. Preference for A and B (3 species):

Caloplaca pyracea (1.7), *Lecanora pulicaris* (2.5), *Lecidella euphorea* (2.5)

3. Preference for B (16 species):

Bacidia circumspecta (0.4), *Caloplaca cerina* (2.9), *C. furfuracea* (2.1), *Candelariella xanthostigma* (0.4), *Heterodermia speciosa* (0.4), *Lecanora allophana* (0.4), *L. chlarotera* (0.4), *Leptogium tenuissimum* (0.4), *Megaspora verrucosa* (0.4), *Peltigera didactyla* (0.4), *P. rufescens* (0.4), *Physcia adscendens* (2.5), *Physciella chloantha* (0.4), *Physconia hokkaidensis* (1.7), *Placynthiella dasaea* (0.4), *P. uliginosa* (0.8)

4. Preference for C:

-

5. No preference (3 species):

Biatora chrysantha (2.5), *Lecania erysibe* (0.4), *Lecanora saligna* (2.5)

Table 4

pH and dry-weight related element concentrations of larch bark in the forest interior and at the forest edge to the steppe.

	Forest interior	Forest edge	<i>P</i> ^a
pH (H ₂ O)	3.41±0.00	3.65±0.00	**
pH (KCl)	2.94±0.00	2.94±0.00	*
C (mmol g ⁻¹)	45.3±0.4	45.3±0.4	
N (μmol g ⁻¹)	339±13	430±25	**
P (μmol g ⁻¹)	45.1±2.8	39.4±3.3	
S (μmol g ⁻¹)	12.0±0.6	14.9±1.3	
K (μmol g ⁻¹)	16.3±1.2	15.5±1.3	
Ca (μmol g ⁻¹)	48.6±5.0	84.3±10.5	**
Mg (μmol g ⁻¹)	33.5±1.4	37.5±1.6	
Na (μmol g ⁻¹)	0.35±0.13	0.41±0.18	
Fe (μmol g ⁻¹)	5.90±0.52	7.45±0.94	
Mn (μmol g ⁻¹)	1.64±0.15	1.81±0.09	
Al (μmol g ⁻¹)	14.5±1.4	19.3±2.1	
Zn (μmol g ⁻¹)	0.13±0.02	0.16±0.01	
Cu (μmol g ⁻¹)	0.06±0.02	0.09±0.02	

^a Levels of significance: * $P \leq 0.05$, ** $P \leq 0.01$ (*t*-test; $N=10$).

Table 5

Frequency (in %) of lichen species on lying dead trunks ($N=10$) and the trunks of living trees ($N=20$) of *Larix sibirica* in the forest interior of site 5.

More frequent on deadwood ($N=15$)^a:

Cladonia fimbriata (100/40^{**})^b, *C. pyxidata* s.l. (100/40^{**}), *C. coniocraea* (80/15^{***}), *Lecidella euphorea* (80/0^{***}), *Caloplaca furfuracea* (70/5^{***}), *Lepraria jackii* (70/5^{***}), *Physcia dubia* (70/25^{*}), *Lecanora saligna* (60/0^{***}), *Ochrolechia androgyna* (60/0^{***}), *Rinodina sophodes* (60/0^{***}), *Buellia griseovirens* (50/0^{***}), *Biatora chrysantha* (40/0^{**}), *Lecanora pulicaris* (40/0^{**}), *Xylographa parallela* (40/0^{**}), *Candelariella vitellina* (20/0^{*}), *Placynthiella dasaea* (20/0^{*})

More frequent on living trees ($N=6$):

Melanelixia exasperatula (80/100^{*}), *Xanthoria candelaria* (60/95^{*}), *Bryoria fuscescens* (10/50^{*}), *Lecanora cadubriae* (10/60^{**}), *Hypocenomyce scalaris* (0/30^{*}), *Trapeliopsis flexuosa* (0/70^{***})

No significant test result ($N=25$):

Amandinea punctata, *Arthonia apatetica*, *A. mediella*, *Calcium viride*, *Candelariella reflexa*, *Cyphelium karelicum*, *C. tigillare*, *Hypogymnia bitteri*, *H. physodes*, *Lecanora albellula*, *L. chlarotera*, *L. hagenii*, *L. hypoptoides*, *L. subintricata*, *L. varia*, *Lecidea nylanderii*, *Megaspora verrucosa*, *Ochrolechia microstictoides*, *O. szatalaënsis*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *Physcia stellaris*, *Trapeliopsis granulosa*, *Usnea spec.*, *Vulpicida pinastris*

^a Levels of significance: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ (χ^2 -test).

^b Percentage of inhabited dead trunks/percentage of inhabited living trunks.

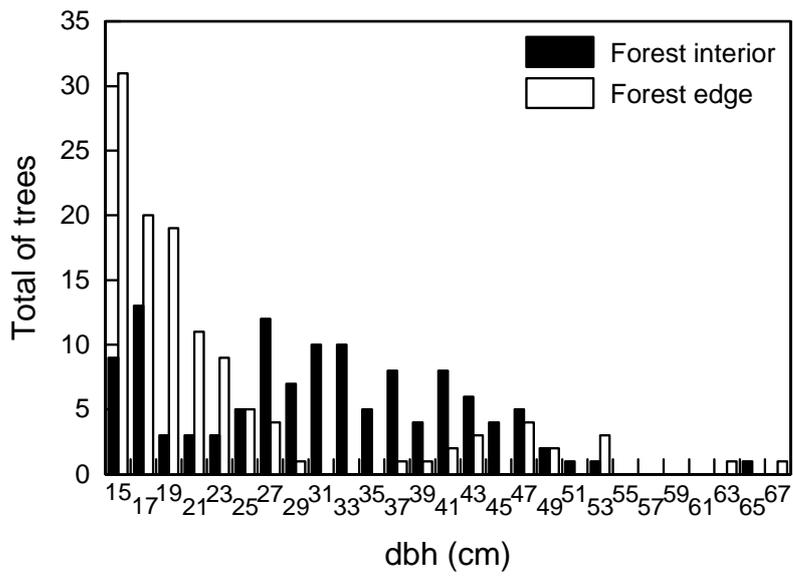


Fig. 1. Distribution of tree diameter classes in the studied larch stands in the forest interior and forest edge. The diameter at breast height (dbh) is divided in classes of 2 cm, with the labels of the axis of abscissas indicated the lower limit of the individual classes.

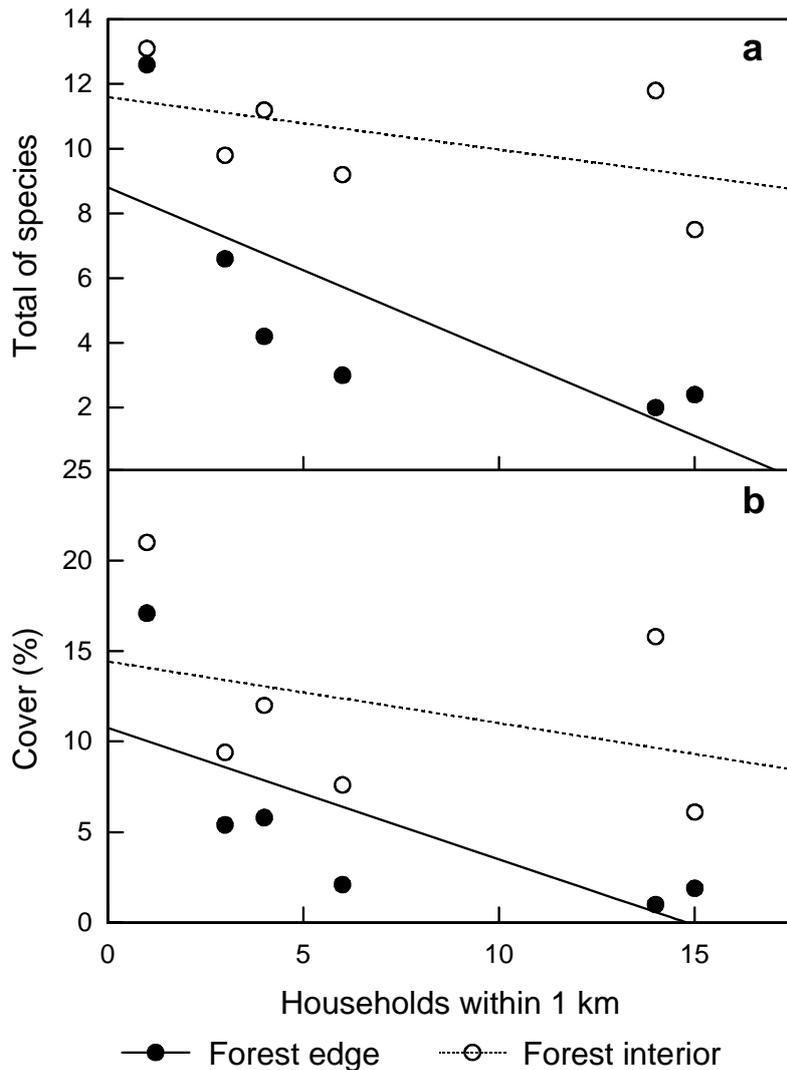


Fig. 2. (a) Total number of epiphytic lichen species and (b) total cover of all lichens on larch trunks ($N=240$; 0 to 1 m above the ground) on each six forest interior and forest edge sites versus the total of households (summer camps of pastoral nomads) within a radius of 1 km from the relevant forest edge plot. Regression lines: (a) forest edge, $y=8.8-0.51x$, $r=-0.75$, $P=0.04$; forest interior, $y=11.6-0.16x$, $r=-0.48$, $P=0.17$; (b) forest edge, $y=10.8-0.73x$, $r=-0.72$, $P=0.05$; forest interior, $y=14.4-0.34x$, $r=-0.36$, $P=0.24$.

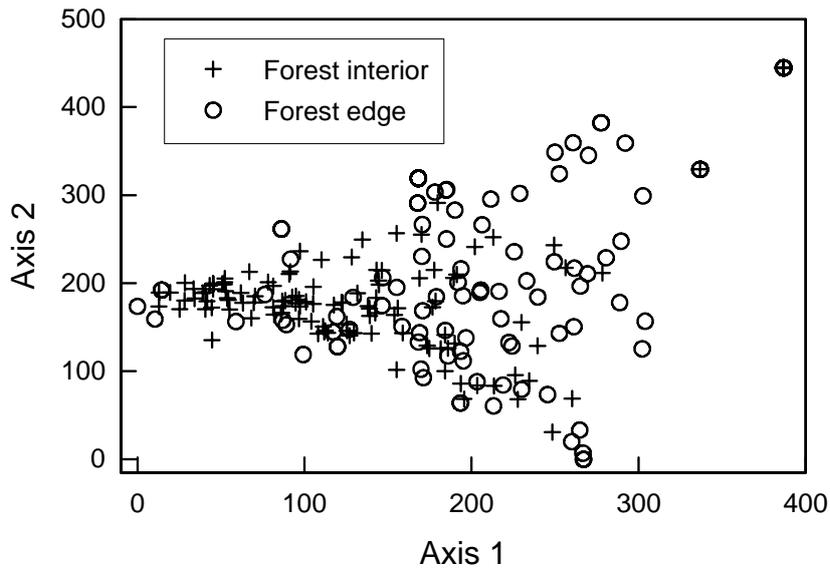


Fig. 3. DCA ordination of *Larix sibirica* trees (N=226) growing in the forest interior or at the edge to the steppe in the Mongolian Altai depending on the individual cover values of the epiphytic lichen species occurring on the lower 1 m of the trunks (64 species). Total variance in species data: 3.86. Eigenvalues: 0.49 (axis 1), 0.31 (axis 2). Length of gradient: 3.87 (axis 1), 4.45 (axis 2). Scaling of axes in SD of species turnover multiplied by 100. Fourteen sample trees were devoid of lichens at the lower trunk and are thus excluded from the analysis.

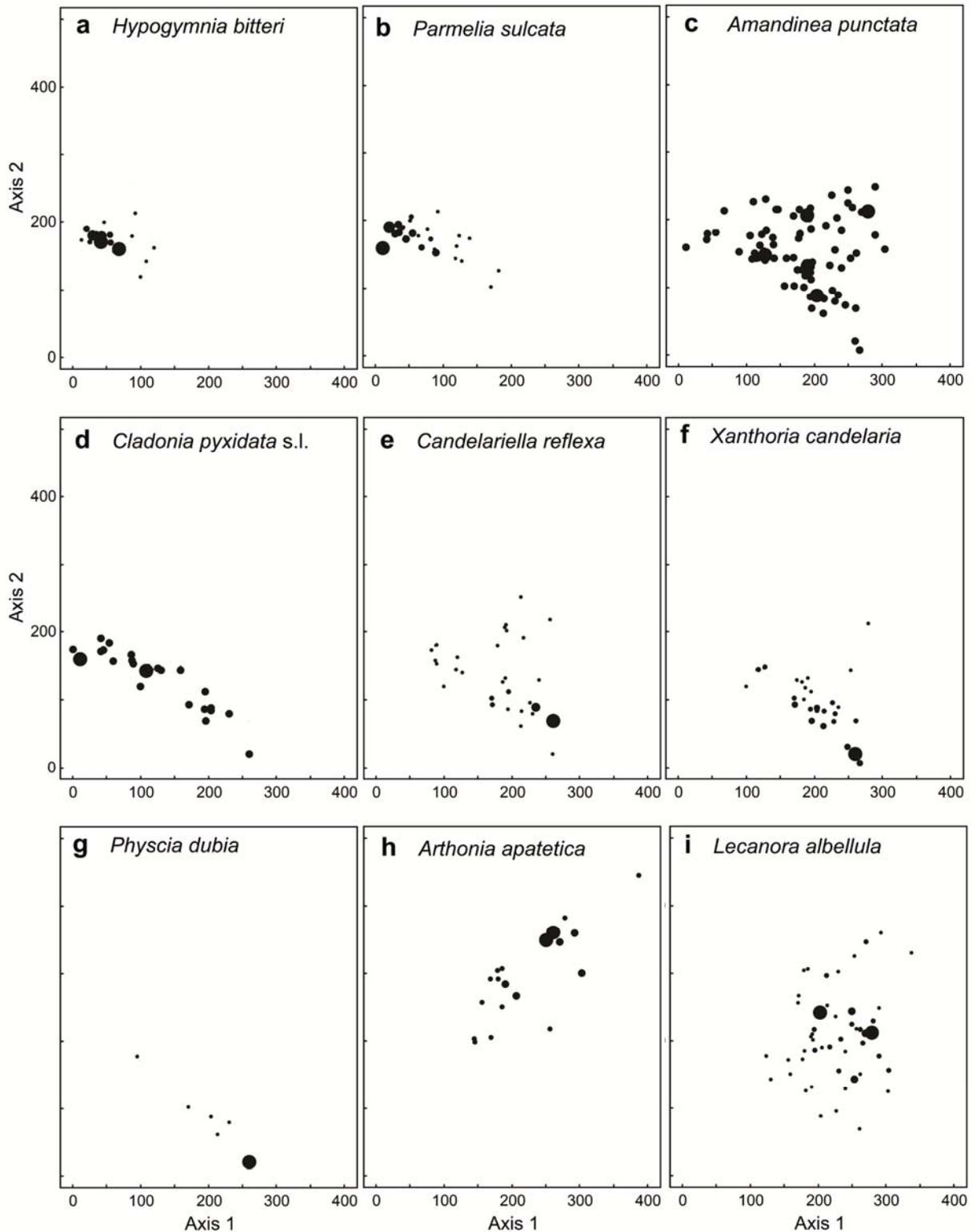


Fig. 4. Distribution of selected species in the DCA ordination space. Dots circles represent trees with an occurrence of the relevant species; dot sizes are proportional to the abundance of the species on the respective tree related to the total of sample trees ($N=226$). Scaling of axes in SD of species turnover multiplied by 100. (a) *Hypogymnia bitteri*, (b) *Parmelia sulcata*, (c) *Amandinea punctata*, (d) *Cladonia pyxidata* s.l., (e) *Candelariella reflexa*, (f) *Xanthoria candelaria*, (g) *Physcia dubia*, (h) *Arthonia apatetica*, (i) *Lecanora albellula*. Fourteen sample trees were devoid of lichens at the lower trunk and are thus excluded from the analysis.

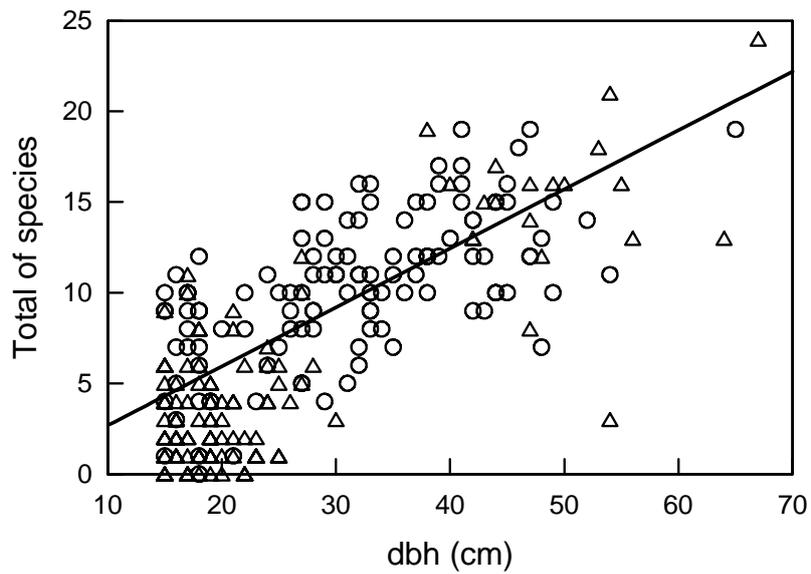


Fig. 5. Total number of epiphytic lichen species (0 to 1 m above the ground) versus the diameter at breast height (dbh) of larch trunks ($N=240$) from the forest interior (circles) and the forest edge (triangles). Regression line: $y=-1.8+0.34x$, $r=0.76$, $P<0.001$. Note that trees with a dbh <15 cm were excluded from lichen recording.