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The epiphytic lichen biota of Caucasian virgin forests: a comparator for European conservation

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Abstract

The north-western Caucasus is exceptional in Europe because of its 1.3 million hectares of unmanaged 'virgin' forest. The Caucasus State Nature Reserve protects some 200,000 hectares, but contiguous areas are exposed to forest loss, fragmentation and degradation. Such an extensive region of virgin forest provides a unique opportunity to document diversity along key ecological gradients for an undisturbed system in Europe. Focusing on lichen epiphytes, we surveyed local diversity hot-spots along a 1200 m altitudinal gradient. Our main results are that: (a) species richness is enormously high in 1-hectare plots (between 233 and 358) representing a new baseline for Europe, (b) species composition differs substantially among plots with turnover increasing for difference in altitude. Cumulative species richness along the gradient was 597. More than a half of detected species had an affinity for, or were restricted to either the lower or the uppermost parts of the altitudinal gradient. However, this was related to differences in forest structure, rather than altitude per se. Species richness in plots increased significantly with the proportion of sparse/open forest. Length of an ecotone line, number of available tree and shrub species and number of dominant tree species also tend to increase species richness. These four variables had higher values at the lower and upper parts of the gradient, than at mid-altitudes, explaining a bimodal relationship of species richness with altitude. We conclude that loss of forest habitat at the lower and upper margins of the altitudinal gradient will cause the most significant decline in epiphytic lichen diversity.

Keywords Altitudinal gradient · Diversity hot-spots · Species richness · Forest structure · Habitat conservation

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Introduction

European ecosystems have been extensively modified over millennia, leading to a landscape that has experienced among the highest global rates of habitat loss, especially deforestation (Hannah et al. 1995; MEA 2005). A 'natural' comparator for European forest diversity is therefore elusive to conservation biologists. For example, areas of intact European 'ancient woodland'—which have high conservation status (Schultze et al. 2014)—are potential remnants of mid-Holocene forest (Peterken 1996; Parviainen 2005), though their diversity is expected to have been: (a) affected by forest loss from the wider landscape, leading to species decline as a consequence of island effects (Hill and Curran 2003; Martensen et al. 2012), and/or (b) have been affected by simplification of forest structure through management (Freemark and Merriam 1986; Cayuela et al. 2006), since remnant woodlands often survived because of their value as an exploitable resource in timber and roundwood. Forest species resilient to these effects may have been more recently impacted by widespread European air pollution (Bobbink et al. 1998). Thus, focussing on lichen epiphytes as bioindicators, recent studies point to an 80% loss of species from the pre- to post-industrial landscapes, caused by pollution and the continuing 20th Century decline of ancient woodland (Ellis et al. 2011, 2018). Nevertheless, these archaeobotanical studies reconstruct diversity for historic landscapes of post-Mediaeval Europe, before industrial pollution, though within a patchwork of fragmented woodlands that had existed for millennia after a Neolithic decline in mid-Holocene forest.

The absence of large tracts of natural forest confounds an ability of European ecologists to examine baseline patterns of diversity with respect to key ecological drivers, such as habitat heterogeneity (Stein et al. 2014), or with respect to altitude/latitude (Sánchez-González and López-Mata 2005; Homeier et al. 2010). Studies on forest diversity that attempt to make these comparisons within a European setting are arguably weakened by their focus on woodland systems that provide data only within the context of large-scale regional deforestation. To approach as far as is possible baseline European forest condition, this study provides underpinning evidence for patterns of diversity in one of the most intact and as yet unexplored forests in Europe. It provides data that highlights the global conservation importance of this forest study system.

The study focused on lichen epiphytes in order to address the extent to which forest diversity is structured by two key ecological processes. First, altitude, which together with latitude captures fundamental processes driving diversity in general (Rahbek 1995; Nascimbene and Marini 2015) and which is hypothesised to structure lichen diversity (Pinokiyo et al. 2008; Baniya et al. 2010). Second, habitat heterogeneity, which has also been shown to control plot scale lichen diversity (Lesica et al. 1991; Gignac and Dale 2005). However, previous studies have conflicted over the relative importance of altitude and habitat heterogeneity (cf. Moning et al. 2009; Bässler et al. 2016); a focus on an intact forest system may help to resolve this debate.

The study examined lichen diversity for the north-western Caucusus, which, together with areas in the boreal zone of Russia and Scandinavia, is the only European region having an extensively intact forest landscape (Potapov et al. 2017). However, the north-western Caucasus has about 1.3 million hectares of intact unmanaged forest (Komarova 2017), which is c. 125 times greater in extent than the next largest examples for other European regions, e.g. Uholka-Shiroki Luh in Ukraine (Commarmot et al. 2013).

The advantage of working in the north-western Caucasus is that—because of their extensively intact nature—local virgin forests have a long altitudinal gradient, and a

natural variability in habitats that is also unaffected by air pollution, providing an excellent system for interrogating baseline diversity trends. The low altitude border of unmanaged forest occurs at about 650 m, with the upper timber line limit at 1900–2000 m. By quantifying habitat heterogeneity of plots nested along an altitudinal gradient, we are able to test which of these effects is most important in structuring lichen diversity.

Materials and methods

Location, plot design, inventory, specimen identification and deposition

Research was performed in the southern temperate forest zone (forests of the Submediterranean type, in the sense of Muesel and Jäger 1989) located within the Caucasus State Nature Reserve (Russia, Republic of Adigea) in the vicinity of Guzeripl (Fig. 1). A mosaic of diverse habitats occurs within forest occupying a 1000 m altitudinal gradient of the study region. Whereas forests dominated by beech (*Fagus orientalis*) and fir (*Abies nordmanniana*) are the most widespread along whole gradient, other forest types are scattered or even frequent, especially at lower and upper altitudes (Zernov 2006). For example sycamore (*Acer trautvetteri*) low forest or birch (*Betula litwinowii*) shrubby forests occur close to the timber line and forests dominated by *Acer campestre*, *Carpinus*, *Fraxinus* and *Quercus* are restricted to lower altitude positions.

Seven square 1-hectare plots were positioned into structurally diverse forest habitats along the altitudinal gradient from 710 to 1910 m. Criteria for plot selection followed the hot-spot approach described by Vondrák et al. (2018). For each plot, different forest types were mapped along with the dominant tree and sub-dominant tree and shrub species (Fig. 2). Areas of these different forest types (Table 1) and the lengths of ecotones were calculated for each plot on the basis of vegetation maps (Fig. 2). Shannon's (H) and Simpson's (d) diversity indices were calculated (cf. data in Table 1). Thus, a set of plot characteristics that, drawing on previous literature, are expected to control lichen species richness were identified (Table 2), and formed the basis of our hypothesis testing.

The survey was done as a multi-expert inventory following methods described by Vondrák et al. (2016), by five of the authors (GU, IU, JM, JV, ZP). Voucher specimens were collected for most of the recorded species (Supplementary Table 1) and are deposited in PRA (JV, ZP), LE (IU) and in personal herbaria of GU and JM. The researchers identified their specimens individually. Numerous specimens, especially sterile crusts, were identified on the basis of thin layer chromatography (TLC). Some specimens were sequenced for nuclear ITS and/or mitochondrial SSU DNA barcode and identified by the standard nucleotide BLAST search. Many recorded species proved to be little-known or even undescribed and are listed along with notes to their identification including TLC data and NCBI accession numbers of DNA sequences (Supplementary Table 2).

Species lists from individual researchers (Supplementary Table 1) were collated into final lists per plots by JM, JV and ZP, and suspicious records were revised. Data for each species include: the list of substrata, presence/absence in plots, and abundance estimations per plot (Supplementary Table 1). Abundances were assessed on a three-class scale: 1—recorded on 1–3 objects ("object" being an individual tree, log, snag, etc.), 2—recorded on 4–10 objects, 3—recorded on more than 10 objects.

Fig. 1 Maps showing the surveyed region and plot locations. Numbering of plots corresponds with Fig. 2

Species richness estimations

Lists of species from individual recorders served as incidence data for estimates of species richness in each plot. We used the estimators Chao2 (Chao 1987), Jackknife1 (Burnham and Overton 1978) and Bootstrap (Chao et al. 2014) implemented in the *specpool* function, package 'vegan' for R (R Development Core Team 2016).

Analysis of beta-diversity

Species composition was compared pairwise among plots, and partitioned into three components (Harrison et al. 1992; Baselga 2010): (a) shared species, i.e. present in both plots,
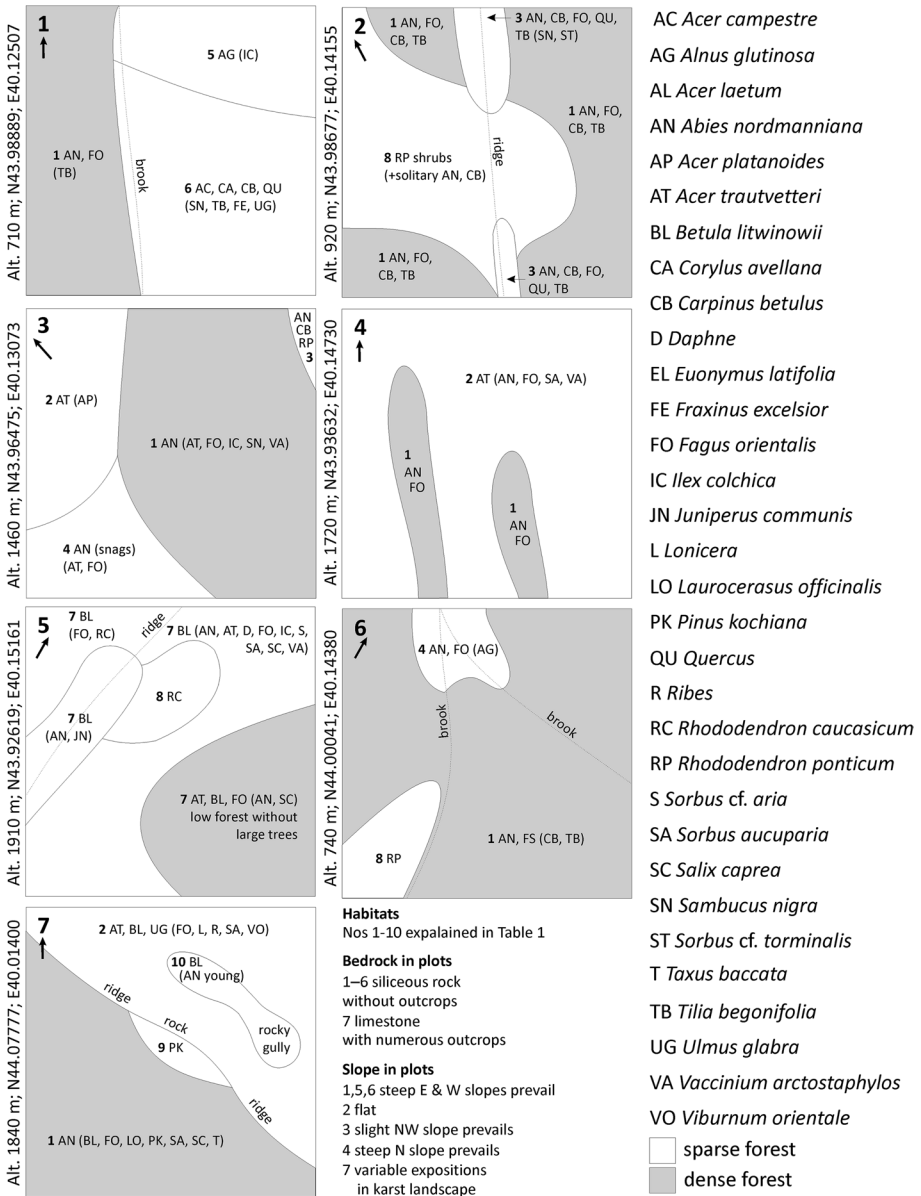
Fig. 2 Forest habitats mapped in each of the seven surveyed plots, including information on dominant and other tree and shrub species

(b) turnover, i.e. species that are substituted in plots, as the number of species in the poorer plot minus number of shared species, and (c) nestedness as the species present only in the richer plot. The three components were analysed separately in relation to pairwise altitudinal difference and habitat dissimilarity. Relationships were tested by Mantel test with 1000 permutations (Mantel 1967).

Table 1 Forest and scrub habitats in the plots. Numbering of plots and habitats corresponds to the values in Fig. 1

No.	Habitat	Occurrence in plots (in m^2)						
		1	2	3	4	5	6	7
1	Dense forest dominated by beech or fir	3342	4914	5999	1580		8352	4966
2	Sparse forest rich in broad-leaved tree species, mostly dominated by sycamore mapple			2220	8420			4143
3	Sparse mixed forest with occurrences of thermophilous tree species as oaks, limes and hornbeams		774	157				
4	Sparse crumbling forest dominated by fir or beech, with numerous snags			1624			753	
5	Sparse flood-plain forest dominated by alder	2142						
6	Sparse alluvial forest with numerous termophilous broad-leaved tree species	4516						
7	Sparse or dense, low subalpine forest, usually dominated by birch					9195		
8	Rhododendron scrubs		4312			805	895	
9	Sparse pine forest on top of limestone rock							298
10	Sparse growth of birch and fir in karst gullies							593

Table 2 Habitat characteristics of selected plots having an impact on local lichen diversity

Plot no. (see Fig. 2)	Altitude (m)	No. of dominant tree species (only trees > 40 cm diam)	All phorophyte species	Area (m^2) of sparse forest with trees > 40 cm diam	Length (m) of eco-tone line	Number of forest types
1	710	6	12	6676	175	3
2	920	5	8	5133	323	3
3	1460	2	9	4031	183	4
4	1720	3	5	8470	275	2
5	1910	0	14	0	329	2
6	740	2	6	1677	169	3
7	1840	5	14	5063	300	4

Table 3 Observed and estimated species richness in plots

	Plot1	Plot2	Plot3	Plot4	Plot5	Plot6	Plot7
Researcher1	175	211	181	215	130	129	221
Researcher2	143	198	178	199	123	136	219
Researcher3	163	212	189	220	129	146	243
Researchers4 + 5	197	209	189	205	140	124	251
Merged observed data	**299**	**342**	**298**	**329**	**233**	**233**	**358**
Chao2 estimation	400	444	340	379	276	297	424
Jackknife1 estimation	394	435	366	401	298	300	439
Bootstrap estimation	346	385	332	365	266	264	398

Merged observed numbers of species are in bold

Species were classified into three groups according to their observed occurrences along the altitudinal gradient: (a) with affinity to upper altitudes, (b) with affinity to lower altitudes, and (c) indifferent to altitude. These were further divided into four sub-classes with respect to species frequencies and abundance scores (Table 4, Supplementary Table 3). Frequency refers to the sum of occurrences in the seven plots (0–7) and abundance score refers to the sum of abundances (0–21) assessed on the three-class scale (see above). Few species occurred outside these categories and were designated as those "with possible preferences to intermediate altitude".

Table 4 Classification of species according to observed frequencies, abundances and occurrences along the altitudinal gradient. Numbers in bold are sums of categories, showing the same relationship to altitude. Criteria for the categories and data relevant to all species are provided in Supplementary Table 3

Groups of species referring to frequency, abundance and occurrence in the altitudinal gradient	Number of species
Frequent and abundant species (throughout altitudinal gradient)	118
Frequent, but not abundant species (throughout altitudinal gradient)	14
Locally common species with occurrence not explained by altitude	24
Uncommon species with occurrence not explained by altitude	124
Species indifferent to altitude	**280**
Locally common species restricted to upper altitudes	29
Uncommon species restricted to upper altitudes	92
Locally common species preferring upper altitudes	50
Uncommon species preferring upper altitudes	15
Species with affinity to upper altitudes	**186**
Locally common species restricted to lower altitudes	18
Uncommon species restricted to lower altitudes	65
Locally common species preferring lower altitudes	24
Uncommon species preferring lower altitudes	11
Species with affinity to lover altitudes	**118**
Species with possible preference to intermediate altitude	**15**

Results

Species richness on a local and altitudinal scale

Species richness in the 1-hectare plots varied between 233 and 358. Species richness estimators each indicated that surveys were not saturated, with a degree of uncovered species richness (Table 3). The lowest numbers of species were recorded from plots at both the lower and upper altitudinal limits: 233 species in a low altitudinal beech-fir forest (Plot 6) and 233 in a subalpine shrub plot (plot 5). The highest species richness was for mixed forest with thermophilous tree species at an intermediate-lower altitude (plot 2, 342 species) and in mixed forest close to the timberline (plot 7, 358 species), with a lower number of species recorded from beech-fir forest at mid-altitudes (plot 3, 298 species). Total species richness accumulated among all plots was 597 species.

Beta-diversity versus altitudinal difference and habitat dissimilarity

Pairwise differences in lichen composition between the plots increased with their difference in altitude (Fig. 3, left), and difference in altitude was positively correlated with turnover in species composition (Mantel test; $r = 0.879$, $P < 0.001$). Thus, total species richness, accumulated among plots, increased with altitudinal difference, while number of shared species decreased. Nestedness appeared to be unrelated to altitude.
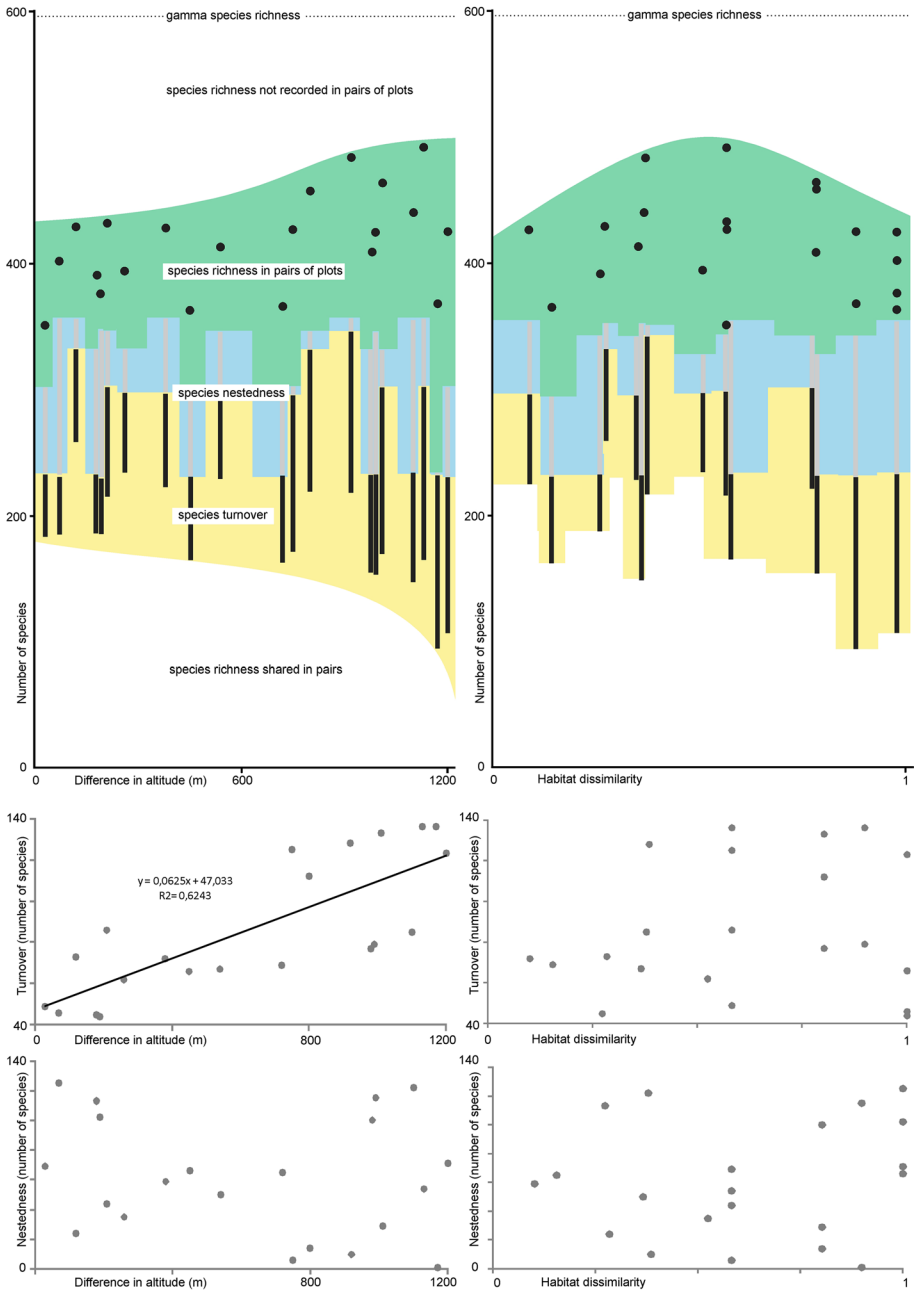
The relationship between habitat dissimilarity and difference in lichen composition was less clearly obvious (Fig. 3, right). With increasing habitat dissimilarity the number of shared species tended to decrease whereas turnover and nestedness tended to increase (but relationships were not statistically significant).

Frequencies and abundances of individual species and their responses to altitude

For the total of 597 species, 20% of species were ubiquitous, and therefore frequent and abundant throughout the altitudinal gradient (118 species). Species that were less common but nevertheless occurred across the altitudinal gradient accounted for 27% of the lichen diversity (162 species). Species with a distinct affinity to upper altitudes accounted for 31% (186 species), and of these 121 species were entirely restricted to upper altitudes. Species with affinities to lower altitudes represented 20% of lichen diversity (118 species), with 83 species entirely restricted to lower altitudes. A lower number of species (2% of lichen diversity) had a preference for intermediate altitudes.

Drivers of species richness

The following variables were tested as drivers for plot scale species richness: (a) altitude, (b) number of available tree and shrub species, (c) number of dominant tree species, (d) proportion of sparse forest with trees > 40 cm in diameter, (e) length of ecotone line and (f) number of forest types, (g) Shannon's index of habitat diversity, and (h) Simpson's index of habitat diversity. The only significant relationship was for the proportion of sparse forest with trees > 40 cm in diameter. Other variables, though not statistically significant, tended

Fig. 3 Relationship of species richness in pairs of plots to the difference in altitude (on the left) and habitat dissimilarity (on the right). Upper charts show the contribution of shared species (white area), species turnover (yellow) and nestedness (blue) to the total pairwise beta-diversity (black dots in the green area). Lower charts show relationships of turnover and nestedness to the difference in altitude and habitat dissimilarity. Only the significant relationship (turnover compared to difference in altitude) is shown with a trend line (see the text for statistical diagnostics). (Color figure online)
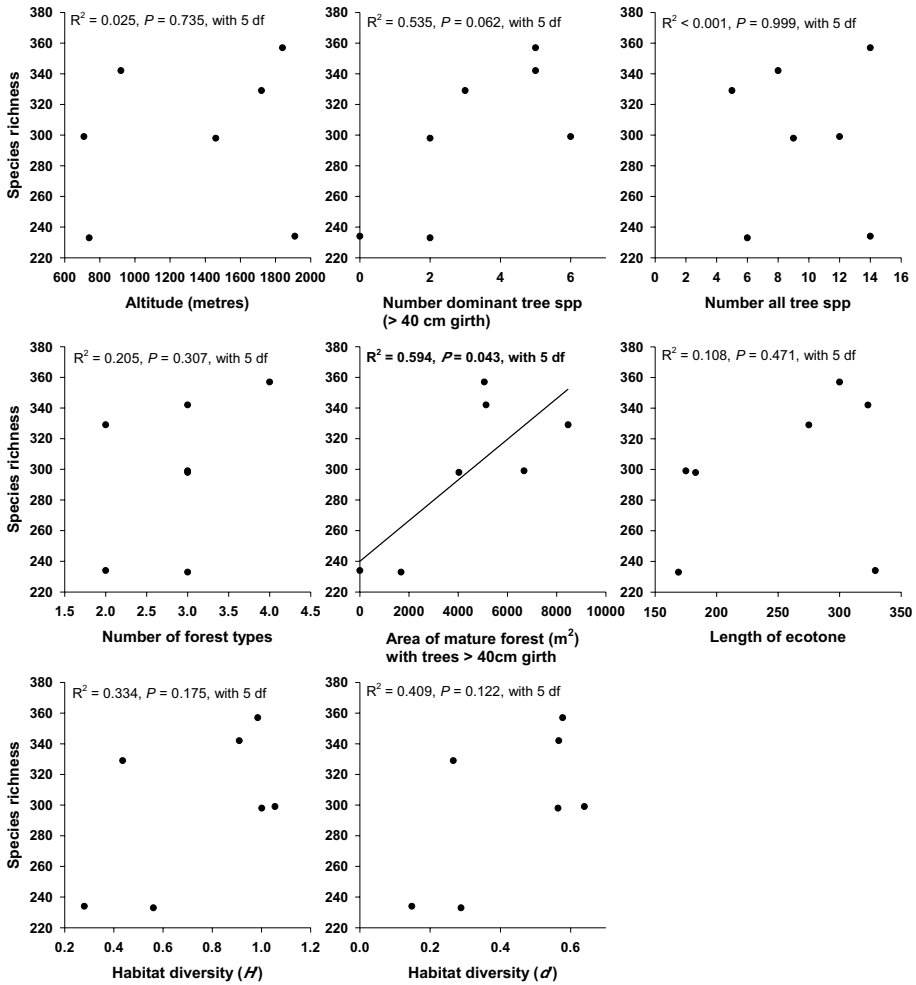
Fig. 4 Explanations for species richness; ordinary linear regression was used to explore the potential contribution of eight hypothesised drivers. Only the statistically significant trend is shown with a trend line

to increase species richness also (Fig. 4). Ecotone length, for example, showed a distinct positive correlation with species richness, but with a mismatch for the species-poor subalpine plot.

Discussion

We provide an estimate of the importance of altitude and habitat heterogeneity controlling lichen epiphyte diversity in natural forest. Our sample size is limited because of the complexity and time constraint in sampling lichens from poorly documented, and complex virgin forest systems; nevertheless, we find no clear linear or unimodal relationship between diversity and altitude, but highlight (i) the role played by contrasting forest types in accumulating species richness through compositional turnover, and (ii) the particular role of

open forest structures increasing diversity. This accords with studies that have demonstrated both community compositional turnover among different forest structures (Barkman 1958; James et al. 1977; Ellis et al. 2015), and the limitation of shading for lichen richness (Marmor et al. 2012; Nascimbene et al. 2012). Perhaps more importantly, we document extremely high levels of plot scale diversity for temperate (Submediterranean) European forest, with a mean of 300 species per 1-hectare square. Although systematic comparisons are difficult, this appears consistent with the number of lichens for the same sampling scale in the tropics (c. 300 species per hectare: Komposch and Hafellner 2000), and supports the emerging idea that 'cryptogamic' species may not conform to 'standard' latitude-diversity gradients (Tedersoo and Nara 2010; Tedersoo et al. 2012). Below we interpret this diversity in greater detail.

Local species richness measured in plots using an identical survey method is available for old-growth forest localities in the Czech Republic (Malíček et al. 2017; unpublished), Ukraine (Vondrák et al. 2018) and the eastern Caucasus (Ismailov et al. 2017, 2019). The numbers reached in these surveys are substantially exceeded by numbers from the plots surveyed in north-western Caucasus (Table 5), and this could be explained by the oceanic climate possibly favourable for poikilohydric organisms, an absence of air pollution, high diversity of local forest habitats, and the unbroken continuity of an extensive forest cover that has maintained species richness (Otte 2007). This includes surprisingly high species richness in the subalpine plot, explained by its transitional position between forest and alpine vegetation that supported a co-occurrence of epiphytes from both vegetation types.

It is difficult to compare plots from this study with those from other regions that have used both different sampling strategies and taxonomic concepts. Moreover, undescribed and tentatively identified species present in our datasets are not listed in most studies from other regions. Nevertheless, as a preliminary comparison (cf. Table 6) we highlight lichen diversity for selected regions in the British Islands (Sanderson 2010), Central Europe (Berger et al. 2018; Cezanne et al. 2008; Cieśliński 2003; Groner 2016; Hofmann 1993; Vondrák et al. 2015, 2016, 2018), Italy (Puntillo 1996) and Spain (Etayo 1989; Gómez-Bolea 1985). According to existing data, Central European forests have distinctly lower numbers of species, whereas numbers from the Mediterranean/west European areas approach the regional species richness from our Caucasian research. For example, Etayo (1989) reports 585 epiphytic lichen species from northern Navarra, which corresponds to the highest regional richness described from European studies. However, this and other inventories (also Puntillo 1996; Gómez-Bolea 1985) generally consider much larger areas and include epiphytes recorded outside forests. Adjusting for sampling effort, the higher numbers of lichen epiphyte species in the Caucasus and other Mediterranean/Submediterranean regions correspond with biodiversity patterns for vascular plants in Europe (Barthlott et al. 2007).

Focussing in detail on plot scale variability, there appeared to be a bimodal pattern in species richness along the altitudinal gradient (Fig. 5a). This is explained by the forest structural variables affecting species diversity, rather than a climatic/mechanistic relationship. Thus, peaks and troughs in species richness could be related most strongly to: (a) number of dominant tree species > 40 cm in diameter, (b) area of sparse forest with trees > 40 cm in diameter (c) number of all phorophyte species, and (d) length of ecotone line (Fig. 5b). These each had low values in prevailing mid-altitude forests, which tended to be uniform, dominated by fir or beech, with low variability of tree species and forest habitats. Based on our field experience, we suggest that our mid-altitudinal plot (plot 3) faithfully represents the habitat structure over a broad area of mid-altitude forest. Relatively simple habitat conditions can be distributed on slopes down to

Table 5 Local species richness of epiphytic and epixylic lichens in one-hectare hot spots in surveyed old-growth forests in Europe. Ordered by the number of species

Forest type, geography and number of plots	Reference	Number of species
Lowland broadleaf forest, Russia, Dagestan, one plot	Ismailov et al. (2017)	82
Mixed low-altitudinal broadleaf forest, Czech Republic, one plot	Malíček et al. (2017)	153
Supramontane spruce forests, Czech Republic, ten plots	Malíček, Palice, Vondrák, unpublished	80–156
Montane pine and birch forest, Russia, Dagestan, one plot	Ismailov et al. (2019)	179
Montane forests dominated by beech, Czech Republic, eleven plots	Malíček, Palice, Vondrák, unpublished	100–190
Montane forests dominated by beech, Ukraine, Carpathians, four plots	Vondrák et al. (2018)	181–228
Montane to subalpine forests, Russia, Adigea, seven plots	This study	**233–358**

Data from our research are in bold

Table 6 Regional species richness of epiphytic and epixylic lichens detected by surveys of old-growth forests in Europe. Ordered by the number of species. Note that regional estimates are for areas larger than the plots used in this study

Forest type, geography and number of plots	Reference	Approximate area (Km^2)	Number of species
Lowland broadleaf forests, Soutok Moravy a Dyje, Czech Republic	Vondrák et al. (2016)	30	212
Spruce-beech-fir dominated montane forest, the Alps, Austria	Berger et al. (2018)	4	274
Montane forests dominated by beech, Stužica/Stuzhytsia, Slovakian and Ukrainian Carpathians	Vondrák et al. (2015)	32	278
Various lowland forests, Białowieża, eastern Poland	Cieśliński (2003)	580	296
Various montane forests, Bödmerenwald-Silberen, Switzerland	Groner (2016)	24	336
Prevailing oak-hornbeam forests, Odenwald, Germany	Cezanne et al. (2008)	>100	356
Various montane forests, western Tyrol, Austria	Hofmann (1993)	≫100	360
Montane forests dominated by beech, Uholka, Ukrainian Carpathians	Vondrák et al. (2018)	23	387
Various forests, Catalania, Spain	Gómez-Bolea (1985)	≫100	410
Various forests, Calabria, Italy	Puntillo (1996)	≫100	412
Lowland broadleaf forests, New forest, South England, United Kingdom	Sanderson (2010); Sanderson in litt.	30	456
Various forests, northern Navarra, Spain	Etayo (1989)	≫100	585
Montane to subalpine forests, Russia, Adigea, data from seven plots	**This study**	**c. 30** (sampled in 7 hectares)	**597**

Data from our research are in bold
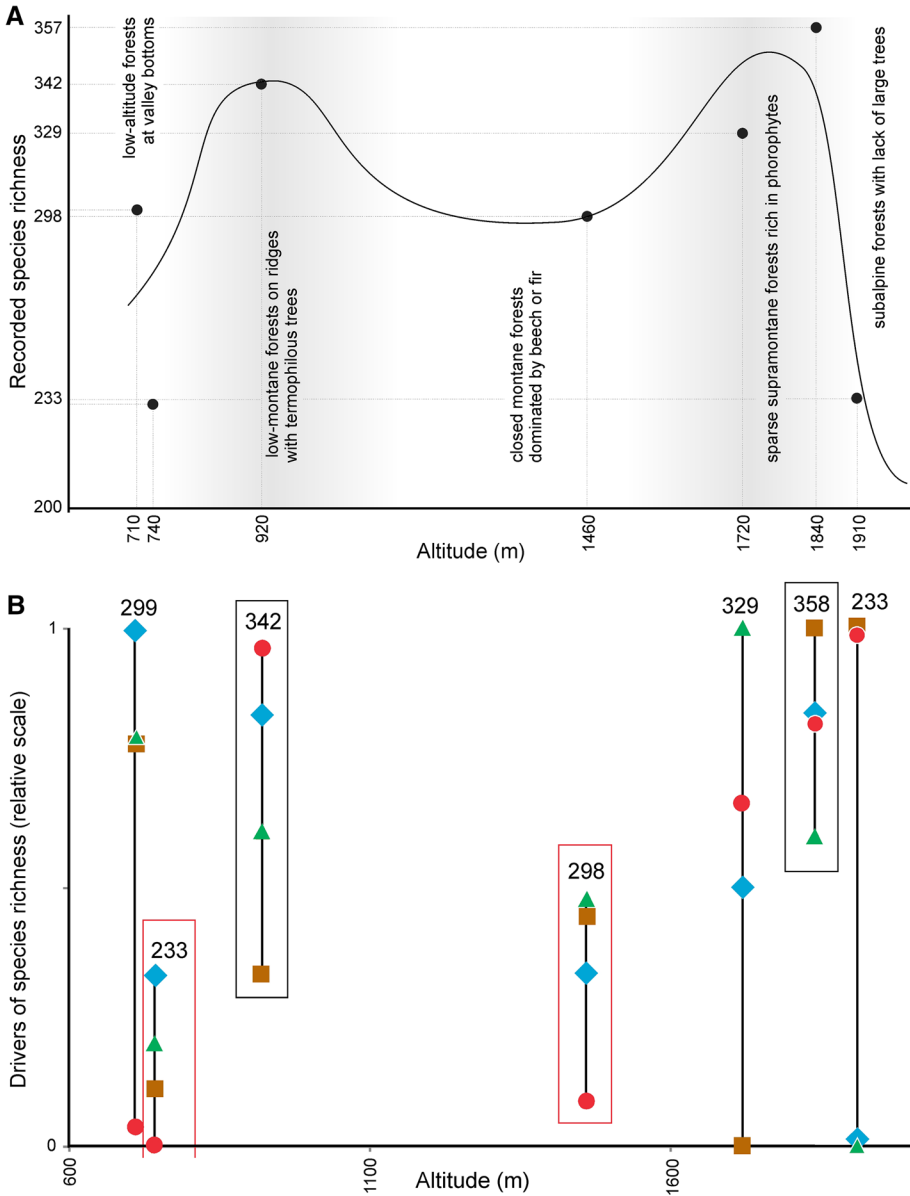
Fig. 5 Species richness and its putative drivers along the investigated altitudinal gradient. **a** Recorded numbers of species in plots along the gradient (dots) approximated by a hand drawn bimodal curve (hypothetical response of species richness to altitude). **b** Four supposed drivers of species richness along the altitudinal gradient. Blue oblique squares—number of dominant tree species (only trees > 40 cm in diameter considered); green triangles—area of sparse forest with trees > 40 cm in diameter; brown squares—number of all phorophyte species; red circles—length of the ecotone line. All drivers are transferred to a relative scale: 0—lowest value, 1—highest recorded value. Primary data for the putative drivers are given in Table 2 and in Fig. 2. Numbers of species per plot are shown, with species poor plots as red squares, rich plots as black squares. (Color figure online)

the lower edge of the altitudinal gradient (plot 6). Diversity hot-spots at lower altitudes tended either to be located along mountain ridges with natural forest gaps and a locally increased diversity of thermophilous trees (plot 2), or in alluvial forests with enriched diversity of habitats and tree species (plot 1). Epiphytic lichens appeared to be most diverse in the upper parts of the altitudinal gradient where the forests were more open with a substantial contribution of sycamore (plot 4) and greater tree diversity (plot 7). The number of lichen species dropped significantly with the sudden shift to subalpine scrub forests at the timber line. Forests at the uppermost part of the gradient (plot 5) may be rich in tree and shrub species and also diverse in habitats, which encourages occurrence of lichens including alpine epiphytes absent from lower parts of gradient. However, the lack of large trees with specific microhabitats explains an absence of numerous old-growth forest lichens. Long-lasting snow cover is known to be a constraining factor (e.g. Bidussi et al. 2016) and probably, together with strong winds and extremely low winter temperatures, decreases the number of species in subalpine lichen communities too.

A lower number of species at middle-altitudes is not unexpected. A "U-shaped" relationship between altitude and species richness is occasionally reported for herbaceous plants, explained by a dense bamboo understory in mid-altitude forests (Černý et al. 2013) or by a strong dominance of beech shading the forest floor (Hrivnák et al. 2011). The latter case seems to provide reasonable explanation for patterns among epiphytic lichens in the north-eastern Caucasus. Alternatively, studies have provided detailed assessments of changes in lichen diversity along altitudinal gradients in European forests (Bässler et al. 2016; Nascimbene and Marini 2015; Nascimbene and Spitale 2017) observing a positive relationship between species richness and altitude. In these cases fewer species recorded at lower altitudes is usually explained by insufficient humidity, which is supposed to be limiting for lichens. In the north-western Caucasus, humidity is high along whole altitudinal gradient (average annual precipitation 1100–2000 mm; Ivanchenko et al. 1982; Akatov 2009) and perhaps does not represent a limiting factor.

Overall, the study highlights the importance of forest diversity in the north-western Caucasus, and provides insight into conservation strategy. Only about 15% of the large and diverse forests of the north-western Caucasus are protected in the Caucasus State Nature Reserve (Kavkazskiy Zapovednik), established in 1924 and declared as a UNESCO Biosphere Reserve in 1979 (Price 2000). The integrity of these forests remain threatened because of logging activities in contiguous areas; according to Karpachevskiy et al. (2015), 43500 hectares of old-growth forests was lost from the north-western Caucasus in the period 2000–2013. Other sources suggest loss of 2100 hectares of natural forest related to the building of infrastructure for the Sochi's Olympic Games in years 2007–2016 (Khoroshev 2017). Within this development footprint, more than 200 small forest fragments were created, each with an area of fewer than 4.5 hectares (Ivonin and Egoshin 2012).

Relevant to this pattern of change, we found that the richness of lichen species was exceptionally high in all plots along the 1200 m long altitudinal gradient. However, most lichen epiphytes were not equally distributed along the gradient, and therefore species composition and richness differ considerably among local plots. We observed that a substantial proportion of species (more than a half) had an affinity for or were restricted either to the lowest or the uppermost parts of the gradient (Table 4). The turnover in species composition was significantly correlated with the increase of altitudinal difference between plots (Fig. 3). The two latter findings suggest a loss of species when the gradient is shortened, including through fragmentation in given altitudinal belts. Habitats at the lower and upper parts of the gradient have to be maintained in order to sustain epiphytic lichen diversity.

Nevertheless, some species are restricted to the central part of the gradient (Table 4) which implies a necessity for habitat conservation along the entire altitudinal range.

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