



Refugial ecosystems in central Asia as indicators of biodiversity change during the Pleistocene–Holocene transition

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ABSTRACT

Site-scale species richness (alpha diversity) patterns are well described for many present-day ecosystems, but they are difficult to reconstruct from the fossil record. Very little is thus known about these patterns in Pleistocene full-glacial landscapes and their changes following Holocene climatic amelioration. However, present-day central Asian ecosystems with climatic features and biota similar to those of the full-glacial periods may serve as proxies of alpha diversity variation through both space and time during these periods. We measured alpha diversity of vascular plants, bryophytes, macrolichens and land snails, as well as environmental variables, in 100-m² plots located in forests and open habitats in the Russian Altai Mountains and their northern foothills. This region contains adjacent areas that possess climatic and biotic features similar to mid-latitude Europe for both the Last Glacial Maximum and contemporaneous Holocene ecosystems. We related alpha diversity to environmental variables using generalized linear models and mapped it from the best-fit models. Climate was identified as the strongest predictor of alpha diversity across all taxa, with temperature being positively correlated to number of species of vascular plants and land snails and negatively correlated to that of bryophytes and macrolichens. Factors important for only some taxa included precipitation, soil pH, percentage cover of tree layer and proportion of grassland areas in the landscape around plots. These results, combined with the high degree of similarity between the current Altai biota and dry-cold Pleistocene ecosystems of Europe and northern Asia, suggest that vascular plant and land snail alpha diversity was low during cold phases of the Pleistocene with a general increase following the Holocene climatic amelioration. The opposite trend probably existed for terricolous bryophytes and macrolichens.

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1. Introduction

The transition from the cold and dry Late Pleistocene climate to the warm and wet Holocene climate resulted in dramatic

biodiversity shifts (Roberts, 1998). In northern Eurasia good community-level data documenting these changes exist for Late Pleistocene mammals (Markova et al., 2008; Pavelková Řičánková et al., 2014, 2015) and in some places for Pleistocene to early Holocene land snails (e.g. Ložek, 2001; Moine, 2014). These snail data indicate an increase in species richness following the Pleistocene–Holocene transition (Juříčková et al., 2014). However, almost no reliable data exist for plant communities during this

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period. Estimations of plant species richness based on the fossil pollen record are problematic because of taphonomic biases and poor taxonomic resolution with some pollen types representing dozens to hundreds of species (Birks et al., 2016). Moreover, pollen records from the full-glacial are relatively rare in northern Eurasia. While analyses of ancient DNA from permafrost provide more reliable information on the Late Pleistocene plant species diversity (Willerslev et al., 2014), such data are limited to permafrost regions.

In the absence of reliable fossil record, species richness variation between the full-glacial and post-glacial periods can be estimated through contemporary proxies, such as present-day ecosystems that are similar to the reconstructed full-glacial ecosystems, both in terms of their climate and occurrence of relict species (Chytrý et al., 2010). For comparative purposes, an ideal situation exists when such ecosystems with full-glacial attributes are adjacent to ones with Holocene features such as higher temperature, higher precipitation and more extensive forest cover, because such adjacent ecosystems are less likely to differ in potentially confounding evolutionary or migration histories. Such a unique situation exists in the Altai Mountains of southern Siberia. The northern part of these mountains and adjacent foothills are relatively warm (January mean temperature above -15°C , July mean above 18°C) and humid, with annual precipitation locally exceeding 800 mm, which are the highest values in Siberia. This area harbours various temperate forest species such as the broad-leaved deciduous tree *Tilia sibirica* (Ermakov, 1998). Several mesophilous herbs typical of European temperate deciduous forests reach their eastern distribution limit in the Altai or are disjunct ca. 2000 km from the eastern limit of their continuous ranges in the Southern Ural Mountains (Ermakov, 1998). The adjacent south-eastern part of the Russian Altai, however, represents a climatic analogue to the dry-cold Pleistocene landscape of mid-latitude Europe. In the basins it is characterized by less than 180 mm of annual precipitation and very low winter temperatures (January mean below -22°C), though summers are relatively warm (July mean up to 16°C). Temperatures are lower on mountain ranges around these basins. These characteristics are similar to the climatic reconstructions of the Last Glacial Maximum climatic reconstructions in various parts of northern Eurasia, particularly the loess landscapes of mid-latitude Europe (Gent et al., 2011). As a result, the south-eastern Russian Altai represents a unique example of a full-glacial palaeoregion that extends over landscape scales (macrorefugium; Nekola 2013). It harbours relict populations of many species that were typical of the last full-glacial period including vascular plants (Pelánková and Chytrý 2009; Magyari et al., 2014; Horsák et al., 2015), land snails (Horsák et al., 2010, 2015; Hoffmann et al., 2011) and mammals (Pavelková Řičánková et al., 2014, 2015). While these characteristic glacial species are common in the south-eastern Russian Altai, they are quite rare or absent from the northern Altai.

Here we consider the south-eastern Russian Altai as a Pleistocene-like landscape, and the northern Altai as a Holocene landscape. We use this unique adjacency to estimate potential changes in site-scale species richness (alpha diversity) and regional species richness (gamma diversity) during the transition from the Pleistocene full-glacial to the Holocene. We focus on vascular plants, bryophytes and macrolichens, which determine ecosystem structure, and land snails, which are important palaeoecological indicators.

2. Study area

The study area (Fig. 1; 49.26–54.77°N, 84.15–88.72°E) comprises the Altai Mountains in the Altai Republic of the Russian Federation, lower mountain ranges north of the Altai (including the Salairskii Kryazh and Gornaya Shoriya), and their respective

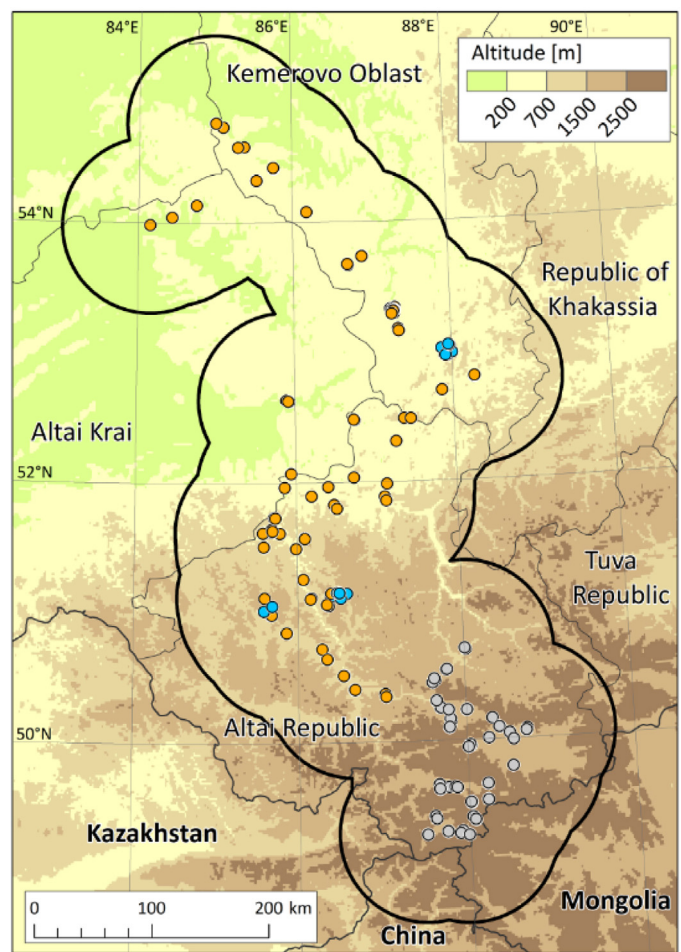


Fig. 1. Map of the study area in southern Russia with sampling sites and limits of the area used for modelling defined by 75 km distance from the nearest sampling site (black line). Sampling location colours represent the three main climate types (brown: mesic-warm, blue: wet-cold, grey: dry-cold). Wet-cold climates are represented by three isolated areas above the timberline. (For interpretation of the references to colours in the figures and figure legends in this paper, the reader is referred to the web version of this article.)

foothills. While the foothills are at altitudes below 300 m, the highest peak of the Altai reaches 4506 m. The highest summits are covered by mountain glaciers (Klinge et al., 2003). We studied the areas up to 2950 m. Following the increase in altitude, temperatures in the study area sharply decrease from the lowlands in the NNW to the mountains in the SSE, from July temperatures above 18°C and January temperatures above -15°C to below 8°C and -30°C , respectively. Annual precipitation locally exceeds 800 mm in the northern Altai foothills and sharply decreases towards the south-east, with arid intermontane basins receiving less than 180 mm (Beresneva, 2006). Temperature and precipitation tend to be positively correlated across the Russian Altai, though there are exceptions especially on higher mountains in the north where temperature is low and precipitation is high.

The hills to the north of the Altai are predominantly covered with forests of *Abies sibirica*, *Betula pendula*, *Picea obovata*, *Pinus sibirica*, *P. sylvestris* and *Populus tremula*. These possess an herb layer very similar to contemporaneous mesic European broadleaved temperate forests (Ermakov, 1998). The central part of the study area contains forest-steppe (or forest-tundra at higher altitudes), i.e. a landscape mosaic with steppe patches on dry south-facing slopes and woodland dominated by *Larix sibirica*, *Picea obovata* and *Pinus sibirica* on north-facing slopes. While this area is drier and colder, its climatic and biotic features still generally correspond to cur-

rent (i.e. Holocene) ecosystems in parts of northern Eurasia. The southern part of the Russian Altai is predominantly comprised of open steppe and tundra grasslands, locally with small *Larix sibirica* woodlands along streams and on north-facing slopes (Kuminova, 1960; Hais et al., 2015, 2016). This area is characterized by a relict biota typical of the European Late Pleistocene full-glacial (Horsák et al., 2010, 2015; Pavelková Řičánková et al., 2014).

The dominant bedrock includes granites and various Palaeozoic sediments. However, there is no remarkable contrast in geology between the northern and south-eastern part of the area (www.geokniga.org/mapstable). The human impact on ecosystems is generally weak, though grasslands are used as cattle and horse pastures. Alien plant species are nearly absent with the exception of some river floodplains and the immediate vicinity of human settlements.

3. Methods

3.1. Data sampling and compilation

We sampled vascular plant, bryophyte, macrolichen and land snail community compositions across the main climatic gradient from the warm and wet landscapes north of the Altai Mountains to cold and dry landscapes in the south-eastern Russian Altai. The sites along this gradient were selected to cover the entire range of available natural ecosystems. At each site, we established 100-m² sample plots located across the maximum available range of topographic positions (e.g. ridge, N-facing slope, S-facing slope, valley bottom). Individual plots were located within patches of homogeneous vegetation, avoiding sharp ecotones, human-made habitats and strongly disturbed vegetation (e.g. recently logged or burned forests). Sampling was done in June–August of 2005, 2006, 2011 and 2012.

In each plot we recorded all species of vascular plants (hereafter ‘plants’) and terricolous (ground-dwelling) bryophytes and macrolichens (hereafter ‘lichens’). Species growing exclusively on woody plants, dead wood or bare rock were not recorded. We refer to bryophytes and lichens as ‘cryptogams’, while cryptogamic vascular plants (lycophods and pteridophytes) were included with vascular plants. A subset of plots within a given site were also sampled for land snails (hereafter ‘snails’). Larger species were searched for by eye by a single observer for 30–60 min per plot, covering all appropriate microhabitats. Small snails (e.g. <5 mm in maximum dimension) were recorded by collecting ~3 litres of leaf litter, moss polsters and topsoil. Wetland litter samples were processed via wet sieving (Horsák et al., 2015) while dry litter was processed using standard protocols (Nekola and Coles 2010). Taxonomy and nomenclature follow Cherepanov (1995) for plants, Ignatov and Afonina (1992) for bryophytes, Andreev et al. (1996) for lichens, and Sysoev and Schilevko (2009) and Nekola et al. (2015) for snails.

The following environmental variables were recorded from each plot: (1) Altitude was read from a GPS device. (2) Slope and aspect were measured with a clinometer and compass, and combined into topographic indices of radiation and heat following McCune and Keon (2002, Eq. 3). (3) Soil depth was measured using a metal rod at four randomly selected spots within each plot and averaged; soils deeper than 30 cm were assigned a value of 30 cm. (4) Soil pH and electrical conductivity were determined from soil samples taken at a depth of 5–15 cm at four randomly chosen locations within each plot, which were mixed, leached in distilled water (soil:water ratio of 2:5), and measured using a Greisinger GPRT 1400 AN pH-meter and Snail Instruments CM113 conductivity meter. (5) Canopy density was recorded using hemispheric canopy photographs (see Chytrý et al., 2007, 2010 for methods) and also estimated visually as percentage tree layer cover in the vertical

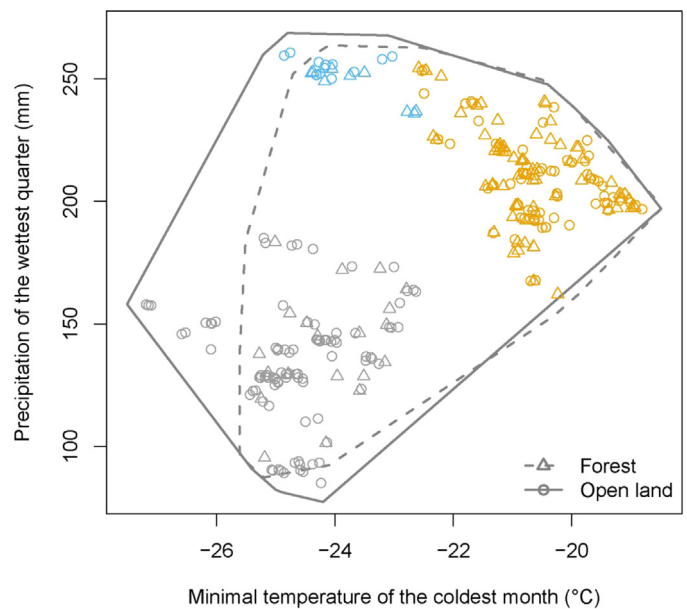


Fig. 2. Position of sampled plots in temperature vs. precipitation space. Colours represent the three climate types (brown: mesic-warm, blue: wet-cold, grey: dry-cold). Convex hulls for forest (dashed) and open-land (solid) plots delimit the climatic space used for alpha diversity mapping.

direction. (6) Macroclimatic data were obtained from the WorldClim database (www.worldclim.org; Hijmans et al., 2005) and data on annual potential evapotranspiration and climatic aridity from the CGIARCSI database (<http://csi.cgiar.org/Aridity>; Trabucco et al., 2008). (7) To account for possible effects of the structure of the surrounding landscape on site diversity, we visually estimated the percentages areas of forest and grassland within 500 m of each plot using Google Earth images.

We sampled 569 plots, which we classified into forest, open-land (grassland and scrub) and mire (peatland). Because mire plots were few and their moisture was largely determined by local topography and aquifer geology and not regional climate, these plots were excluded from further analysis. Following preliminary exploratory analyses all plots not sampled for snails were also excluded. This did not significantly change results of the analyses for plants and cryptogams as snail plots were located at all sampling sites and represented all habitat types. In the end 102 forest plots and 174 open-land plots were analyzed.

3.2. Statistical analysis

We modelled alpha diversity (species counts in 100-m² plots) for each taxon as a function of the explanatory variables described above using generalized linear models (GLM; McCullagh and Nelder 1989). Before model selection we performed the following exploratory data analyses: (1) Cleveland dot plots of all the variables to assess their distribution and identify outliers; (2) pair plots to assess the collinearity among predictors and the shape of the relationships between response variables, predictors and geographical coordinates; (3) conditional graphs to identify potential interactions. Based on this we removed several collinear variables, especially various measures of temperature and precipitation.

Exploratory analyses indicated a dominant effect of climate on alpha diversity and existence of three climate types (Figs. 1 and 2; Fig. S1 in Appendix A in Supplementary data): (1) mesic-warm; low altitudes in the northern Altai and hilly areas north of the Altai; (2) wet-cold; the alpine belt in the northern Altai; (3) dry-cold; mountain plateaus, ranges and intermountain basins in the south-eastern

Russian Altai. We used these three climate types as an additional model predictor.

Most models of alpha diversity were fit with negative binomial error distribution, but Poisson error distribution was used for snails. We used stepwise selection based on likelihood ratio tests to find the best model for each response variable. Possible terms after the removal of intercorrelated variables included the main predictor variables (minimum temperature of the coldest month, precipitation of the wettest quarter, soil pH, tree layer cover, proportion of grassland area in plot surroundings, and climate type), second-order polynomials where suggested by data exploration, and identified interactions: temperature \times pH, temperature \times precipitation, temperature \times climate type, and precipitation \times climate type. As we intended to interpolate predicted alpha diversity across the whole study area based on climatic variables, the starting model for stepwise selection included temperature and precipitation together with the climate type as the main terms, their interactions, and second-order polynomials if suggested by the data exploration. These terms were then sequentially removed and at each step the model was tested against each of a set of simpler models until the omission of any term led to a significant decrease in explained variation. At that point the selected terms of climatic predictors were kept in the model (climate type could always be removed), while the other predictors were sequentially added and removed until the inclusion of another term did not cause a significant improvement in the current model and, simultaneously, the omission of any term did not lead to significant worsening.

We examined the final model residuals with respect to fitted values and individual predictors and checked them for spatial autocorrelation using variograms. We also checked residuals for normality, homogeneity of variance and influential observations. Because lichens were absent from many forest plots, their model residuals deviated from normality. Therefore we fitted an alternative model of presence/absence of lichens with binomial error. However, as the inference remained the same, we present the original models for alpha diversity with negative binomial error. In other models we did not identify any serious violation of model assumptions, although some residual spatial autocorrelation remained, indicated by sigmoid variograms. While this suggested existence of alternating areas with underestimated and overestimated alpha diversity, further examination indicated that this did not cause any serious model flaws.

For alpha diversity mapping, models were simplified by removing non-climatic explanatory variables for which maps were unavailable across the study area. Predicted alpha diversity values were projected on the WorldClim-based maps of climatic variables. To avoid unrealistic extrapolations, we mapped predicted values only within 75 km from the nearest sampling site. In addition, we mapped predicted alpha diversity values only in areas with those combinations of temperature and precipitation that were either encountered or could be interpolated (not extrapolated) from sampled sites. The mapped combinations were defined using convex hull drawn around the sampling sites, separately for forest and open-land sites, in a space defined by temperature and precipitation (Fig. 2).

In addition to alpha diversity, we also assessed regional species richness (gamma diversity of Whittaker 1972; not Cody 1985) among the three climate types using sample-based rarefaction (Colwell et al., 2004). Cumulative numbers of species recorded within plots belonging to each climate type and habitat (forest vs. open land) were computed and rarified to nine plots, which was the lowest number of plots found among the climate type-habitat combinations.

To assess potential effects of nested community structure on species richness, we identified diagnostic and constant species

for forest and open-land plots within each of the three main climate types. We calculated the phi coefficient of association and defined diagnostic species as those with $\Phi > 0.25$, disregarding non-significant associations ($P < 0.05$, Fisher's exact test; Tichý and Chytrý, 2006). Calculations were done for equalized numbers of plots within climate types. Diagnostic species with the highest Φ values are characterized by the strongest concentration of their occurrence within particular climate types. In addition, we defined constant species as those occurring in $>40\%$ plots of each climate type-habitat combination; such species are frequent, though not necessarily concentrated in these combinations.

GLMs were computed and graphs drawn using R 3.2.3 (www.r-project.org) with the MASS (Venables and Ripley, 2002), ncf ver. 1.1–5 and gstat (Pebesma, 2004) packages. GIS analyses were performed using ArcGIS 10.3 (www.esri.com). Rarefaction and diagnostic and constant species were computed using the JUICE program (Tichý 2002).

4. Results

All taxa exhibited considerable alpha diversity variation, both between forests and open-land habitats and among climate types (Table 1). Individual taxon/habitat models explained 11.7–40.3% of variation (Table 2). Models for bryophytes explained less variation than for the other taxa.

Climatic factors were identified as the dominant driver of alpha diversity across all taxa in both forests and open habitats (Table 2, Figs. 3 and 4). Minimum temperature of the coldest month (representing a set of correlated temperature variables) significantly affected all groups and entered all the models except that for open-land snails. However, while alpha diversity of plants and snails increased with temperature, that of bryophytes and lichens decreased. Precipitation of the wettest quarter (representing a set of correlated precipitation variables) also influenced alpha diversity, although its effect was weaker and non-significant in some cases. All significant precipitation effects were positive, although in some cases (especially in the models for marginal effects) alpha diversity began to decrease in highest precipitation areas, especially at high altitudes in the north where high precipitation was coupled with low temperature. Alpha diversity was further influenced by soil pH, with unimodal response in plants and snails and negative response in bryophytes and lichens.

The maps (Fig. 5) showed higher alpha diversity of plants and snails in the northern Altai and its foothills, i.e. the landscape with Holocene conditions, and lower alpha diversity in the Pleistocene-like landscape of the south-eastern Russian Altai. For bryophytes and lichens these patterns were reversed.

The three climate types differed in gamma diversity (regional species richness), expressed as rarified cumulative number of species across plots (Table 1). Mesic-warm conditions had the highest gamma and alpha diversity of plants, while the wet-cold conditions had the lowest gamma diversity, though their alpha diversity was intermediate in forests. In cryptogams gamma and alpha diversity patterns coincided, with the mesic-warm conditions being poorest, the wet-cold conditions being richest for bryophytes and the dry-cold conditions for lichens. Gamma and alpha diversity of forest snails was low in the wet-cold conditions and higher in the other two climate types. In contrast, their gamma and alpha diversity on open land was low in both wet-cold and dry-cold conditions, while being high in mesic-warm conditions. For all taxa each climate type contained specific species that tended to be absent elsewhere (Table 1, Table S1 in Appendix A in Supplementary data), indicating the presence of species turnover between areas with contrasting climate.

Table 1

Mean, minimum and maximum numbers of species in 100-m² plots (alpha diversity), rarified cumulative numbers of species recorded across all forest or open-land plots (gamma diversity), and diagnostic and constant species related to the three climate types of the Russian Altai. Cumulative numbers were rarified to 9 plots in all cases, which is the minimum number per habitat (forest vs. open land) and climate type. Lower and upper limits of the 95% confidence interval for rarefaction are given. Full list of diagnostic and dominant species is in Table S1 in Appendix A in Supplementary data.

Habitat type	Forest			Open land		
Climatic type	Mesic-warm	Wet-cold	Dry-cold	Mesic-warm	Wet-cold	Dry-cold
No. of plots	73	9	20	68	13	93
Vascular plants						
Mean no. of species per 100 m ²	48.9	38.6	32.1	47.3	30.0	30.1
Min. no. of species per 100 m ²	28	8	9	13	8	6
Max. no. of species per 100 m ²	80	56	59	90	42	63
Rarified no. of species	206	133	189	263	134	189
Lower confidence interval	183	110	166	238	113	170
Upper confidence interval	230	156	211	288	155	208
No. of diagnostic species	65	26	66	106	65	44
No. of constant species	27	37	4	5	17	0
Bryophytes						
Mean no. of species per 100 m ²	6.7	12.8	9.7	4.0	8.5	5.1
Min. no. of species per 100 m ²	0	6	2	0	4	0
Max. no. of species per 100 m ²	26	18	17	10	15	19
Rarified no. of species	38	56	48	27	57	34
Lower confidence interval	29	41	37	20	43	26
Upper confidence interval	47	71	60	34	70	42
No. of diagnostic species	4	18	14	1	18	1
No. of constant species	1	9	4	0	0	0
Lichens						
Mean no. of species per 100 m ²	0.4	1.8	3.2	0.7	2.1	2.9
Min. no. of species per 100 m ²	0	0	0	0	0	0
Max. no. of species per 100 m ²	7	6	15	6	6	17
Rarified no. of species	4	12	23	5	12	20
Lower confidence interval	1	5	15	2	6	14
Upper confidence interval	6	19	30	9	19	26
No. of diagnostic species	0	1	4	0	3	4
No. of constant species	0	0	0	0	0	0
Snails						
Mean no. of species per 100 m ²	7.2	3.8	4.7	5.3	2.4	1.5
Min. no. of species per 100 m ²	1	0	1	0	0	0
Max. no. of species per 100 m ²	11	7	13	12	8	10
Rarified no. of species	19	11	21	22	11	10
Lower confidence interval	11	4	13	14	5	5
Upper confidence interval	27	18	29	30	17	14
No. of diagnostic species	9	1	11	11	4	4
No. of constant species	8	4	2	3	1	0

Table 2

Marginal (gross) effects of the variables used in the models of alpha diversity (site-scale species richness) of the four taxa, each assessed separately for forest and open habitats, and partial effects of these variables in the models. Temperature = minimum temperature of the coldest month; Precipitation = precipitation of the wettest quarter; Grassland = proportion of grassland area within 0.5 km from the plot location. The values are squared deviances (D²), corresponding to the proportion of explained variation. Significance levels: *** P < 0.001, ** P < 0.01, * P < 0.05, ns = not significant, na = not applicable.

		Temperature		Precipitation		Soil pH		Tree cover		Grassland		Total	Shared
Marginal (gross) effects													
Vascular plants	Forest	0.334	***	0.148	***	0.066	*	0.072	*	.	ns	na	na
	Open	0.227	***	0.118	***	0.255	***	.	ns	0.101	***	na	na
Bryophytes	Forest	0.093	***	.	ns	0.096	**	0.095	***	.	ns	na	na
	Open	0.041	**	.	ns	0.069	***	.	ns	.	ns	na	na
Lichens	Forest	0.251	***	.	ns	0.058	*	0.263	***	.	ns	na	na
	Open	0.215	***	0.040	*	0.097	***	.	ns	.	ns	na	na
Snails	Forest	0.215	***	.	ns	0.094	***	0.104	***	0.156	***	na	na
	Open	0.213	***	0.328	***	0.047	**	.	ns	0.124	***	na	na
Partial effects													
Vascular plants	Forest	0.334	***	.	ns	.	ns	.	ns	.	ns	0.334	na
	Open	0.028	**	0.033	**	0.083	***	.	ns	.	ns	0.376	0.232
Bryophytes	Forest	0.045	*	.	ns	.	ns	0.047	*	.	ns	0.140	0.048
	Open	0.103	***	0.076	***	.	ns	.	ns	.	ns	0.117	−0.062
Lichens	Forest	0.090	**	.	ns	.	ns	0.103	**	.	ns	0.353	0.160
	Open	0.291	***	0.116	***	.	ns	.	ns	.	ns	0.331	−0.076
Snails	Forest	0.132	***	.	ns	.	ns	.	ns	0.073	**	0.288	0.082
	Open	.	ns	0.239	***	0.035	**	.	ns	0.041	***	0.403	0.087

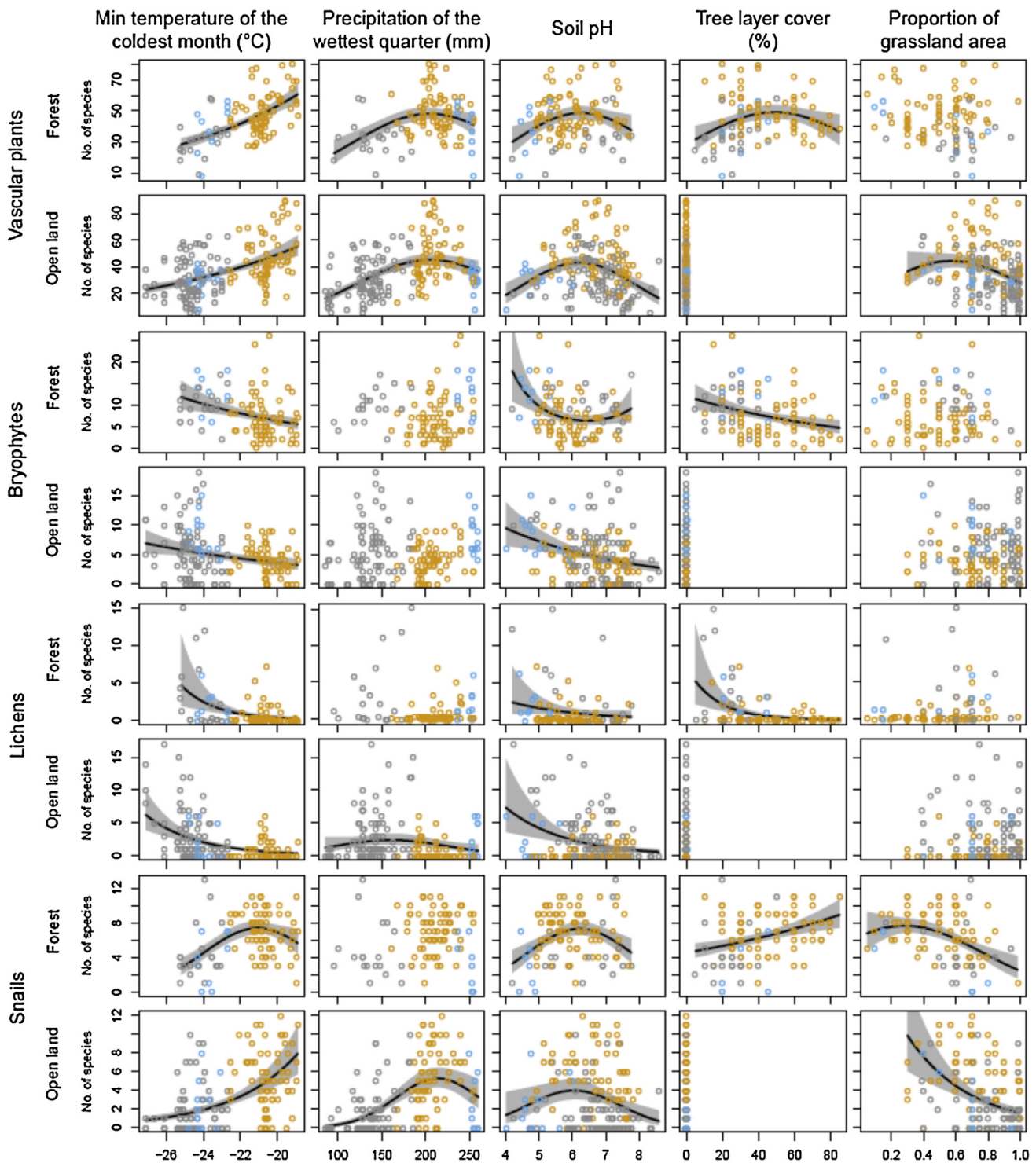


Fig. 3. Generalized linear models (GLM) for marginal (gross) effects of the variables used in the final models of alpha diversity (no. of species in 100-m² plots). Colours represent the three climate types (see Figs. 1 and 2). Grey area indicates the approximately 95% pointwise confidence interval. Trends are not fitted for non-significant relationships ($P > 0.05$). For forest lichens the points are slightly jittered because of many zeros.

5. Discussion

5.1. Macroclimatic effects on species richness

The climatic contrast between mesic-warm vs. dry-cold environments is the main driver of both alpha diversity (site-scale species richness) and gamma diversity (regional species richness) between northern landscape with Holocene features and the

south-eastern Pleistocene-like landscape in the Russian Altai. A strong decrease in alpha diversity of vascular plants and snails was observed from the mesic-warm forests and open habitats in the north to both the alpine belt of the northern Altai (wet-cold, also Holocene features) and the high-mountain plateaus and basins of the south-eastern Russian Altai (dry-cold, Pleistocene-like landscape). While the northern areas contain forests with the highest known vascular plant alpha diversity in extratropical Eurasia

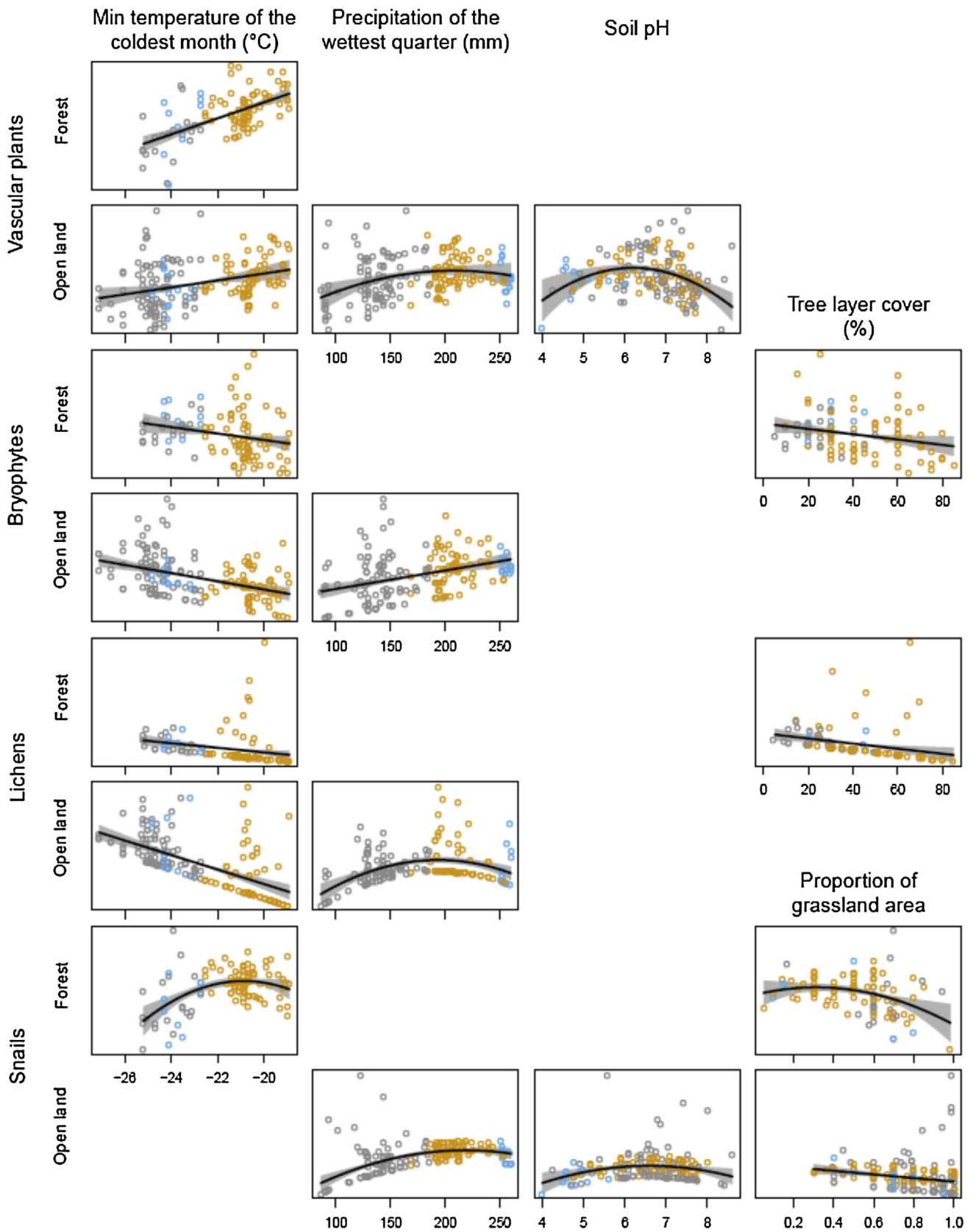


Fig. 4. Partial effects of variables used in the GLMs of alpha diversity after accounting for the effects of other variables used in the models. Variables not entering particular models are not shown. See Fig. 3 for details.

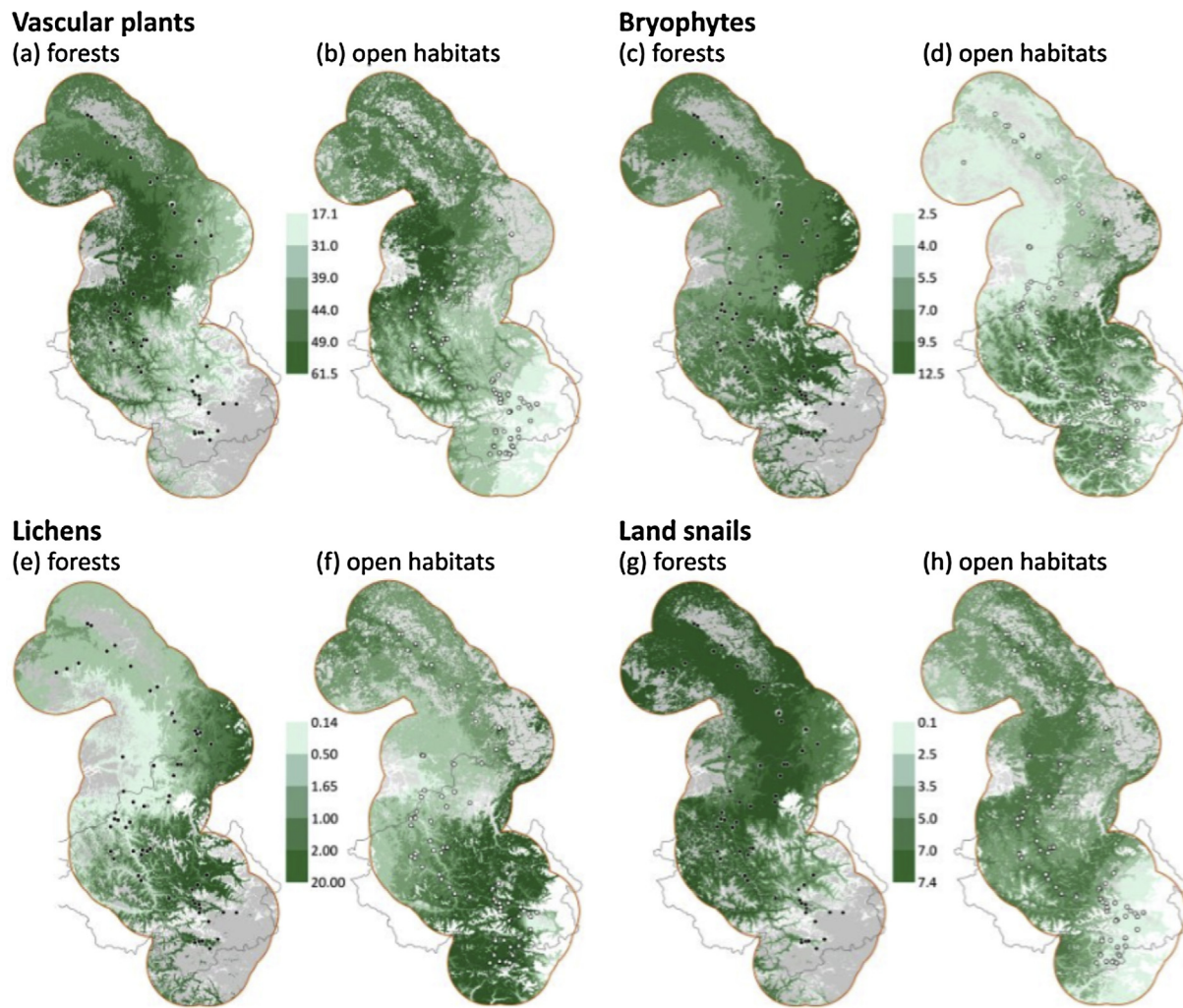


Fig. 5. Alpha diversity modelled by GLMs for the Russian Altai Mountains and adjacent areas in the north. Intensity of green colour indicates the number of species (note different scales for individual taxa). Grey areas are those with less than 2% of forests and less than 2% of open habitats, respectively. White areas were not modelled because their climate was different from the climate of the sampling sites (areas outside the convex hull in Fig. 2). The mapped area is delimited in Fig. 1; sampling sites (points) and the border of the Altai Republic (light grey line) are shown.

(Chytrý et al., 2012), some plant communities in the southeast are depauperate with snails being absent from many sites. Our models showed that this pattern is dominantly controlled by macroclimate, especially temperature and also to some extent by precipitation.

Decrease in alpha and gamma diversity with increasing altitude, or increase at mid-altitudes with subsequent decrease, is a well-known phenomenon for many taxa across the globe (Rahbek, 1995; Grau et al., 2007). Possible reasons include (1) harsher climate, (2) low environmental heterogeneity or (3) limited total habitat area at higher altitudes, (4) dispersal limitation on isolated mountains, and (5) geometric constraints such as the mid-domain effect (Colwell and Lees, 2000; but see McClain et al., 2007). While providing plausible explanations for lower alpha and gamma diversity in plants and snails in the isolated wet-cold mountains of the northern Altai, most of these factors (except climatic harshness) cannot explain differences observed between low-altitude (mesic-warm) areas in the northern Altai and high-altitude (dry-cold) areas in the south-east. The south-eastern areas are environmentally heterogeneous, spatially extensive, and do not represent isolated mountain tops. Mid-domain effects probably also cannot provide a plausible explanation for their lower alpha and gamma diversity because the sampled species-poor sites in the south-east were still far below the upper border of the local altitudinal domain: the glacier-snow line

at ca. 3200–3300 m (Klinge et al., 2003). This suggests that climate is the main driver of the differences in alpha and gamma diversity between the Holocene and Pleistocene-like landscapes in the Russian Altai.

A potential additional explanation for lower alpha and gamma diversity of plants and snails in the south-eastern Russian Altai is the migration lag due to longer persistence of Last Glacial Maximum (LGM) mountain glaciers as compared to the mesic-warm north (Blomdin et al., 2016). However, models suggest that LGM vegetation similar to contemporaneous south-eastern Altai vegetation likely occurred next to these glaciers (Hais et al., 2015). Migration lag in the south-eastern Altai thus should not be large, at least not much larger than in the northern Altai. Moreover, migration lag may be more important for gamma than alpha diversity (Stewart et al., 2016). Unlike alpha diversity, gamma diversity in the south-east is not so much lower than in the north, suggesting little effect of glaciation history.

Additionally, if the alpha and gamma diversity pattern was driven mainly by migration lag, community structure would tend to be nested. We found no evidence for this. Species-poor communities of plants and snails in the areas with wet-cold and dry-cold climate are not just depauperate subsets of the communities in the area with mesic-warm climate. On the contrary, they are char-

acterized by several species that are rare or absent in the areas with mesic-warm climate. Many of these species are characteristic of European LGM loess assemblages (Table S1 in Appendix A in Supplementary data; Horský et al., 2010, 2015; Hoffmann et al., 2011).

Alpha and gamma diversity of terricolous cryptogams (bryophytes and lichens) in the Altai respond to the same environmental drivers as those of plants and snails, but conversely are highest in colder areas. Increasing cryptogam gamma diversity towards harsher climates, or at least its slower decrease than in vascular plants, has been observed when moving from lower to higher latitudes (Rozzi et al., 2008; Bültmann, 2010; Mateo et al., 2016). Cryptogam alpha and gamma diversity also often peaks at higher altitudes than that for vascular plants in montane districts (Grytnes et al., 2006; Grau et al., 2007). There are two potential reasons for this pattern. First, cryptogams appear to be better adapted to lower temperatures (Furness and Grime, 1982), perhaps reflecting an evolutionary origin of lichen and moss lineages during colder periods of the earth's history (Romdal et al., 2013). The strong response of cryptogam diversity to temperature, found in this and other studies (e.g. Spitale, 2016), supports this explanation. Second, there can be indirect effect through competition: vascular plants grow better in warmer areas and thus tend to outcompete cryptogams via shading. This was seen in the Altai where minimum terricolous cryptogam alpha diversity was observed under the densest tree canopy. In Altaian open habitats, bryophyte alpha and gamma diversity also tended to increase towards precipitation-richer areas, reflecting the generally high moisture requirements of bryophytes, although many of them are desiccation-tolerant (Proctor and Tuba, 2002). In general, alpha and gamma diversity patterns in cryptogams point to the role of macroclimate as the main driving factor.

5.2. Other factors affecting species richness

Soil pH, tree canopy cover and proportion of grassland area in the surrounding landscape were also found to correlate with (and possibly drive) alpha diversity in some situations. While cryptogam alpha diversity tended to decrease with pH, this trend disappeared after accounting for climate. The covariance of acidic soils with high precipitation likely reflects increased cation leaching rates. Plant and snail alpha diversity demonstrated a unimodal response to pH. In the nearby and ecologically similar Western Sayan Mountains, this pattern was explained by high stress in both low and high pH soils. In low pH soils the stress can be due to release of toxic elements such as aluminium, while in the high pH soil, the stress can be caused by drought associated with such soils (Chytrý et al., 2007). However, in the Altai unimodal alpha diversity–pH relationships were preserved after accounting for precipitation, suggesting that soil pH also has independent effects on species richness. Palpurina et al. (2017) yielded the same result for alpha diversity across Eurasian steppes. Snail alpha diversity decrease on high pH soils on the Altaian open land is also probably partly related to the toxic increase of soil salinity.

Finally, the proportion of grassland area in the landscape appeared to have a negative effect on snail alpha diversity. To some extent, this may be caused by different transpiration rates in open and forested landscapes, which influence local moisture patterns. Such patterns can remarkably affect snail communities, although they cannot be predicted from precipitation data (Hoffmann et al., 2011).

5.3. Species richness of the full-glacial vs. post-glacial landscapes

Our view of the contemporaneous Russian Altai biota as representing a proxy for the Pleistocene full-glacial to Holocene

transition in mid-latitude Europe is supported by the presence of cold and drought adapted species assemblages typical of the European LGM loess landscapes in the southeast (Horský et al., 2010, 2015; Magyari et al., 2014; Pavelková Řičánková et al., 2014, 2015) and mesophilous thermophilous species in the north of the area (Ermakov, 1998). If valid, this perspective suggests that plant and snail alpha diversity during cold phases of the Pleistocene was on average lower than during interglacials (including the Holocene), both in forests and open habitats. This prediction is consistent with several independent pieces of evidence from the fossil record. First, DNA barcoding of Arctic permafrost cores (Willerslev et al., 2014) shows that Arctic plant alpha diversity was higher before the LGM, decreased during the LGM, and increased thereafter. Second, palynological richness estimates from different areas appear to exhibit the same pattern. For example, in formerly non-glaciated areas of Romania, lower palynological richness was noted for colder and drier periods of the Late Glacial (such as the Younger Dryas) with higher richness occurring during warmer and wetter periods (such as Bølling/Allerød and the early Holocene; Feurdean et al., 2012). However, palynological richness can be underestimated in presence of strong pollen producers (such as *Pinus*) which can swamp out other pollen types. Third, the Central European LGM mollusc record, which shares several species with current fauna of the southeast Russian Altai, was also much poorer in species at both local and regional scales than the Holocene record (Mania, 1995; Ložek 2001; Juříčková et al., 2014; Moine 2016). However, we are not aware of any estimates of cryptogam species richness from fossil record for the Late Pleistocene full-glacial period from northern Eurasia.

Plant alpha diversity could also decrease at the Pleistocene–Holocene transition as a result of forest expansion on former grasslands, triggered by climatic amelioration. Boreal and cool temperate forests tend to be locally poorer in species than steppic grasslands because their species pools is generally smaller than that of grasslands. Moreover, many forest species may have been restricted by migration lags during the early Holocene forest expansion. This scenario is consistent with an observation of sharp decrease in palynological richness at a Swiss site where rapid Bølling warming in the Late Glacial led to replacement of the steppe-tundra by scrub and woodland (Ammann et al., 2013). Similar mechanisms can explain higher plant richness in alpine than lowland areas in central Alaska, where alpine grasslands can be relicts of Pleistocene steppe-tundra, whereas lowland steppe tundra was overgrown by forest (Roland and Schmidt, 2015). However, in our current study we made separate comparisons of richness within forests and on open land, aiming to describe species richness change within habitats rather than the change due to replacement of grasslands by forests.

Alpha diversity can also be influenced by the regional species pool (Zobel, 2016). We found coincidence between alpha and gamma diversity of cryptogams, but as in previous studies (e.g. Stewart et al., 2016), there were interesting scale-related differences in other taxa. Although plant alpha diversity tends to be lowest in the dry-cold, Pleistocene-like landscape of the southeastern Russian Altai, gamma diversity is much higher in this region than in the wet-cold mountain areas of the northern Altai. To some extent, this can reflect the isolated nature and smaller areas of the wet-cold mountains and associated island effects which increase extinction rates. However, it may also indicate greater habitat heterogeneity in the dry Pleistocene-like steppe-tundra landscapes, driven by stronger moisture gradients from wet stream floodplains to dry steppic slopes, and the presence of woodland patches in the otherwise treeless landscape (Hais et al., 2016). Such habitat heterogeneity is considered one of the necessary conditions for sustaining not only large-herbivores in the full-glacial landscape (Guthrie, 1990), but also regional plant and snail diversity (Horský

et al., 2015). Full-glacial landscapes may have locally supported poorer plant communities because of drought and cold stress, but the existence of mesic and wet patches in the matrix of dry habitats provided opportunities for survival of many species of contrasting ecology at the landscape scale (Horsák et al., 2015). Also for snails, the lack of shelter and water in open habitats may have eliminated many species from individual sites (Horsák et al., 2010, 2013), but small woodland and wetland patches guaranteed relatively high snail gamma diversity in the otherwise hostile dry-cold LGM landscape.

6. Conclusions

We used a space-for-time substitution approach, involving a unique example of landscape-scale refugium of relict full-glacial biota and an adjacent landscape with Holocene biota to predict alpha diversity changes during the Pleistocene–Holocene transition. While no modern landscape represents a perfect match to LGM conditions, strong biogeographical similarity to the LGM landscapes of mid-latitude Europe exists in the Russian Altai. Our analysis suggests that alpha diversity of plants and snails, and to some extent also gamma diversity of these taxa, were likely considerably lower during the dry-cold phases of the Pleistocene than in the Holocene. In contrast, both alpha and gamma diversity of bryophytes and lichens were probably higher in LGM, reflecting cryptogam cold tolerance. These insights complement fragmentary fossil data on biodiversity change at the Pleistocene–Holocene transition. The Altai macrorefugium serves as a unique window into the biodiversity and ecology of Pleistocene full-glacials. However, fossil data from whole communities with taxonomic resolution to the level of species will be necessary to accurately test predictions made from this proxy system.

Authors' contributions

M.C. and M.Ho. conceived the ideas; M.C., J.D., N.E., D.G., M.H., P.H., M.K., S.K., P.L., Z.P., P.R. and M.V. collected botanical data; M.Ho., V.H. and J.C.N. collected snail data; V.S. performed statistical modelling; O.H. did GIS analyses; M.C. wrote the text with contributions from V.S., M.Ho. and J.C.N.; all authors discussed the results.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.12.033>.

References

Ammann, B., van Leeuwen, J.F.N., van der Knaap, W.O., Lischke, H., Heiri, O., Tinner, W., 2013. Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 391, 40–59.

- Andreev, M., Kotlov, Y., Makarova, I., 1996. Checklist of lichens and lichenicolous fungi of the Russian Arctic. *Bryologist* 99, 137–169.
- Bültmann, H., 2010. Diversity and similarity of lichen floras of countries along a south-north gradient from Italy to Greenland. *Annali di Botanica* 0, 1–10.
- Beresneva, I.A., 2006. Climates of the Arid Zone of Asia. Nauka, Moskva, RU (in Russian).
- Birks, H.J.B., Felde, V.A., Björne, A.E., Grytnes, J.-A., Seppä, H., Giesecke, T., 2016. Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. *Rev. Palaeobot. Palynol.* 228, 1–25.
- Blomdin, R., Heyman, J., Stroeve, A.P., Hättestrand, C., Harbor, J.M., Gribenski, N., Jansson, K.N., Petrakov, D.A., Ivanov, M.N., Alexander, O., Rudoy, A.N., Walther, M., 2016. Glacial geomorphology of the Altai and Western Sayan Mountains, Central Asia. *J. Maps* 12, 123–136.
- Cherepanov, S.K., 1995. Vascular plants of Russia and adjacent countries. Mir i sem'ya-95, Saint Petersburg (in Russian).
- Chytrý, M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Popov, D., Roleček, J., Řezníčková, M., Šmarda, P., Valachovič, M., 2007. Plant species richness in continental southern Siberia: effects of pH and climate in the context of the species pool hypothesis. *Global Ecol. Biogeogr.* 16, 668–678.
- Chytrý, M., Danihelka, J., Horsák, M., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý, L., Martynenko, V.B., Baisheva, E.Z., 2010. Modern analogues from the Southern Urals provide insights into biodiversity change in the early Holocene forests of Central Europe. *J. Biogeogr.* 37, 767–780.
- Chytrý, M., Ermakov, N., Danihelka, J., Hájek, M., Hájková, P., Horsák, M., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., Zelený, D., 2012. High species richness in hemiboreal forests of the northern Russian Altai, southern Siberia. *J. Veg. Sci.* 23, 605–616.
- Cody, M.L., 1985. Towards a theory of continental species diversities. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA, pp. 214–257.
- Colwell, R.K., Lees, D.C., 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* 15, 70–76.
- Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85, 2717–2727.
- Ermakov, N., 1998. The Altaian relict subnival forest belt and the vegetation of pre-Pleistocene mountainous landscapes. *Phytocoenologia* 28, 31–44.
- Feurdean, A., Tămaș, T., Tanțău, I., Fărcaș, S., 2012. Elevational variation in regional vegetation responses to late-glacial climate changes in the Carpathians. *J. Biogeogr.* 39, 258–271.
- Furness, S.B., Grime, J.P., 1982. Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology. *J. Ecol.* 70, 525–536.
- Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R., Lawrence, D.M., Neale, R.B., Rasch, P.J., Vertenstein, M., Worley, P.H., Yang, Z.-L., Zhang, M., 2011. The Community Climate System Model Version 4. *J. Clim.* 24, 4973–4991.
- Grau, O., Grytnes, J.-A., Birks, H.J.B., 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *J. Biogeogr.* 34, 1907–1915.
- Grytnes, J.A., Heegaard, E., Ihlen, P.G., 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecol.* 29, 241–246.
- Guthrie, R.D., 1990. *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. University of Chicago Press, Chicago, IL.
- Hais, M., Komprdová, K., Ermakov, N., Chytrý, M., 2015. Modelling the Last Glacial Maximum environments for a refugium of Pleistocene biota in the Russian Altai Mountains Siberia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 438, 135–145.
- Hais, M., Chytrý, M., Horsák, M., 2016. Exposure-related forest-steppe: A diverse landscape type determined by topography and climate. *J. Arid Environ.* 135, 75–84.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hoffmann, M.H., Meng, S., Kosachev, P.A., Terechina, T.A., Silanteva, M.M., 2011. Land snail faunas along an environmental gradient in the Altai Mountains (Russia). *J. Molluscan Stud.* 77, 76–86.
- Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., 2010. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. *J. Biogeogr.* 37, 1450–1462.
- Horsák, M., Chytrý, M., Axmanová, I., 2013. Exceptionally poor land snail fauna of central Yakutia (NE Russia): climatic and habitat determinants of species richness. *Polar Biol.* 36, 185–191.
- Horsák, M., Chytrý, M., Hájková, P., Hájek, M., Danihelka, J., Horsáková, V., Ermakov, N., German, D.A., Kočí, M., Lustyk, P., Nekola, J.C., Preislerová, Z., Valachovič, M., 2015. European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas* 44, 638–657.
- Ignatov, M.S., Afonina, O.M., 1992. Check-list of mosses of the former USSR. *Arctoa* 1, 1–58.
- Juričková, L., Horsák, M., Horáčková, J., Abraham, V., Ložek, V., 2014. Patterns of land-snail succession in Central Europe over the last 15,000 years: main changes along environmental, spatial and temporal gradients. *Quat. Sci. Rev.* 93, 155–166.

- Klinge, M., Böhner, J., Lehmkuhl, F., 2003. Climate pattern, snow- and timberlines in the Altai Mountains, Central Asia. *Erdkunde* 57, 296–308.
- Kuminova, A.V., 1960. Plant cover of the Altai. SO AN SSSR, Novosibirsk (in Russian).
- Ložek, V., 2001. Molluscan fauna from the loess series of Bohemia and Moravia. *Quat. Int.* 76–77, 141–156.
- Magyari, E.K., Kuneš, P., Jakab, G., Sümegi, P., Pelánková, B., Schäbitz, F., Braun, M., Chytrý, M., 2014. Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? *Quat. Sci. Rev.* 95, 60–79.
- Mania, D., 1995. The influence of Quaternary climatic development on the Central European mollusc fauna. *Acta Zool. Cracov.* 38, 17–34.
- Markova, A.K., van Kolfschoten, T., Bohncke, S., Kosintsev, P.A., Mol, J., Puzachenko, A. Yu., Simakova, A.N., Smirnov, N.G., Verpoorte, A., Golovachev, I.B., 2008. Evolution of European Ecosystems During Pleistocene–Holocene Transition (24–8 kyr BP). KMK Scientific Press, Moscow.
- Mateo, R.G., Broennimann, O., Normand, S., Petitpierre, B., Araújo, M.B., Svenning, J.-C., Baselga, A., Fernández-González, F., Gómez-Rubio, V., Muñoz, J., Suarez, G.M., Luoto, M., Guisan, A., Vanderpoorten, A., 2016. The mossy north: an inverse latitudinal diversity gradient in European bryophytes. *Sci. Rep.* 6, art. 25546.
- McClain, C.R., White, E.P., Hurlbert, A.H., 2007. Challenges in the application of geometric constraint models. *Global Ecol. Biogeogr.* 16, 257–264.
- McCullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*. Chapman & Hall, London.
- McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. *J. Veg. Sci.* 13, 603–606.
- Moine, O., 2014. Weichselian Upper Pleniglacial environmental variability in north-western Europe reconstructed from terrestrial mollusc faunas and its relationship with the presence/absence of human settlements. *Quat. Int.* 337, 90–113.
- Nekola, J.C., Coles, B.F., 2010. Pupillid land snails of eastern North America. *Am. Malacol. Bull.* 28, 29–57.
- Nekola, J.C., Coles, B.F., Horsák, M., 2015. Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *J. Molluscan Stud.* 81, 196–216.
- Nekola, J.C., 2013. Biodiversity refuges (refugia). In: MacLeod, N., Archibald, D.J., Levin, P. (Eds.), *Grzimek's Animal Life Encyclopedia: Extinction*. Gale Publishing, Farmington Hills, MI, pp. 141–148.
- Palpurina, S., Wagner, W., von Wehrden, H., et al., 2017. The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands. *Global Ecol. Biogeogr.*, <http://dx.doi.org/10.1111/geb.12549>.
- Pavelková Řičánková, V., Robovský, J., Riegert, J., 2014. Ecological structure of Recent and Last Glacial mammalian faunas in northern Eurasia: the case of Altai-Sayan refugium. *PLoS One* 9, art. e85056.
- Pavelková Řičánková, V., Robovský, J., Riegert, J., Zrzavý, J., 2015. Regional patterns of postglacial changes in the Palearctic mammalian diversity indicate retreat to Siberian steppes rather than extinction. *Sci. Rep.* 5, art. 12682.
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* 30, 683–691.
- Pelánková, B., Chytrý, M., 2009. Surface pollen–vegetation relationships in the forest-steppe, taiga and tundra landscapes of the Russian Altai Mountains. *Rev. Palaeobot. Palynol.* 157, 253–265.
- Proctor, M.C.F., Tuba, Z., 2002. Poikilohydry and homoihydry: antithesis or spectrum of possibilities? *N. Phytol.* 156, 327–349.
- Rahbek, C., 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18, 200–205.
- Roberts, N., 1998. *The Holocene. An Environmental History*. Blackwell, Oxford.
- Roland, C.A., Schmidt, J.H., 2015. A diverse alpine species pool drives a reversed plant species richness–elevation relationship in interior Alaska. *J. Biogeogr.* 42, 738–750.
- Romdal, T.S., Araújo, M.B., Rahbek, C., 2013. Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecol. Biogeogr.* 22, 344–350.
- Rozzi, R., Armesto, J.J., Goffinet, B., Buck, W., Massardo, F., Silander, J., Arroyo, M.T., Russell, S., Anderson, C.B., Cavieres, L.A., Callicott, J.B., 2008. Changing lenses to assess biodiversity: patterns of species richness in sub-Antarctic plants and implications for global conservation. *Front. Ecol. Environ.* 6, 131–137.
- Spitale, D., 2016. The interaction between elevational gradient and substratum reveals how bryophytes respond to the climate. *J. Veg. Sci.* 27, 844–853.
- Stewart, L., Alsos, I.G., Bay, C., et al., 2016. The regional species richness and genetic diversity of Arctic vegetation reflect both past glaciations and current climate. *Global Ecol. Biogeogr.* 25, 430–442.
- Sysoev, A., Schileyko, A., 2009. *Land Snails and Slugs of Russia and Adjacent Countries*. Pensoft, Sofia.
- Tichý, L., Chytrý, M., 2006. Statistical determination of diagnostic species for site groups of unequal size. *J. Veg. Sci.* 17, 809–818.
- Tichý, L., 2002. JUICE, software for vegetation classification. *J. Veg. Sci.* 13, 451–453.
- Trabucco, A., Zomer, R.J., Bossio, D.A., van Straaten, O., Verchot, L.V., 2008. Climate change mitigation through afforestation/reforestation: a global analysis of hydrologic impacts with four case studies. *Agric. Ecosyst. Environ.* 126, 81–97.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth edition. Springer, New York, NY.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Willerslev, E., Davison, J., Moora, M., et al., 2014. Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506, 47–51.
- Zobel, M., 2016. The species pool concept as a framework for studying patterns of plant diversity. *J. Veg. Sci.* 27, 8–18.