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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-m^2 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.

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 (Juřičková 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 palaeorefugium 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 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.

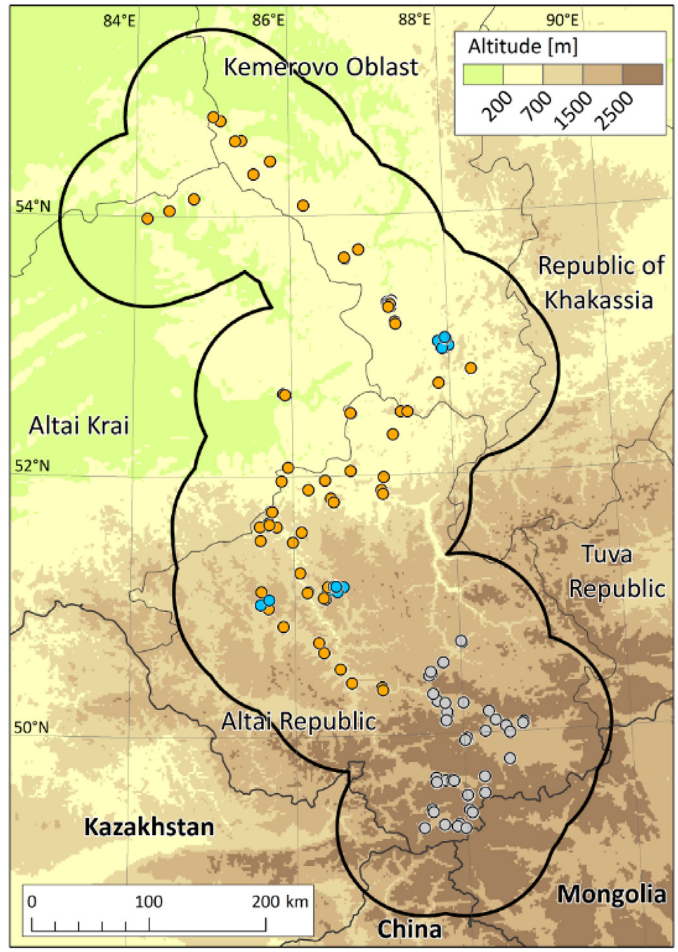

Fig. 1. Map of the study area in southern Russia with sampling sites and limits of the area used for modelling defined by 75 km distance from the nearest sampling site (black line). Sampling location colours represent the three main climate types (brown: mesic-warm, blue: wet-cold, grey: dry-cold). Wet-cold 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.)

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-