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Forest snail diversity and its environmental predictors along a sharp climatic gradient in southern Siberia

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ABSTRACT

Diversity patterns of forest snail assemblages have been studied mainly in Europe. Siberian snail faunas have different evolutionary history and colonization dynamics than European faunas, but studies of forest snail diversity are almost missing from Siberia. Therefore, we collected snails at 173 forest sites in the Russian Altai and adjacent areas, encompassing broad variation in climate and forest types. We found 51 species, with a maximum of 15 and an average of seven species per site. The main gradient in species composition was related to soil pH, a variable that also positively correlates with snail abundances. The second gradient was associated with climate characteristics of winter. We observed significant differences in both species richness and composition among six forest types defined based on vegetation classification. Hemiboreal continental forests were the poorest of these types but hosted several species characteristic of European full-glacial stages of the Late Pleistocene. A high snow cover in Temperate coniferous and mixed forests, protecting the soil from freezing, allowed the frost-sensitive large-bodied (> 10 mm) species to inhabit this forest type. In contrast to most of the European snail assemblages studied so far we found that the factors responsible for the variation in species richness differed from those driving species composition. This may be attributed to the sharp climatic gradient and the presence of the cold-adapted species typical of the Pleistocene cold stages. We suggest that southern Siberian forests hosting these species can serve as modern analogues of full-glacial forests in periglacial Central and Eastern Europe.

1. Introduction

Land snails represent a diverse group of soil-dwelling invertebrates occurring in various forest ecosystems (e.g. Solem, 1984; Barker and Mayhill, 1999; Martin and Sommer, 2004; Cameron et al., 2010; Schilthuizen, 2011). Their communities have been studied in detail particularly in the boreal and temperate zones of Europe (e.g. Wäreborn, 1969; Waldén, 1981; Martin and Sommer, 2004; Hylander et al., 2005; Juřičková et al., 2008; Horsák et al., 2010a). The studies from European boreal and temperate zones congruently show that both snail species richness (i.e. number of species per unit area) and abundance (i.e. number of individuals per unit area) increase with the amount of available calcium. The tendency of species accumulation towards calcium-rich habitats often results in the nested pattern of species composition in the systems without any other strong environmental driver of snail distribution (Hylander et al., 2005; Juřičková et al., 2008). Such nestedness is possible also because of the lack of calcifuge species in Eurasian snail fauna (e.g. Horsák et al., 2013a). Soil moisture has been identified as the second main driver of snail distribution with positive effect on species richness and abundance (e.g. Martin and Sommer, 2004). However, this relationship is less straightforward and less detectable than that for calcium (Hettenbergerová et al., 2013).

In contrast to Europe, there are very limited data on environmental correlates of land snail assemblages in extratropical Asia. Some malacological studies focused on snail diversity in the boreal zone of Siberia (e.g. Horsák et al., 2013b; Horsák and Chytrý, 2014), while others have pointed out potential analogues of the European full-glacial ecosystems in the southern Siberian mountain systems (Horsák et al., 2010b, 2015; Hoffmann et al., 2011; Chytrý et al., 2017). However, the studies from southern Siberia did not focus specifically on the compositional variation in forest snail faunas and its environmental predictors. Chytrý et al. (2017) analysed variation in species richness of land snails and plants across the Altai Mountains and their foothills and found that forest snail

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species richness was driven mainly by minimum temperature of the coldest month. Species richness was also significantly influenced by soil pH, tree canopy cover and proportion of grassland area in the surrounding landscape.

A detailed comparison of environmental correlates of land snail community patterns between southern Siberian and Central European forests is important for several reasons. Firstly, the regional diversity of land snails in southern Siberia is much smaller than at the same latitudes in continental Europe. While the species pool of forest-dwelling snails in temperate Europe is about 500 species (Kerney et al., 1983; Welter-Schultes, 2012), less than 100 species have been reported from southern Siberia (Sysoev and Schileyko, 2009). Secondly, several diverse groups of European snails are entirely missing from Siberia (e.g. Clausiliidae and Helicidae) or are notably less diversified (e.g. Zonitidae), which may be caused by different evolutionary histories of European and Siberian snail faunas. Thirdly, the snail fauna of southern Siberia is composed of species with Palaearctic ranges (shared with Europe), species of Siberian distribution, and cold-adapted species now extinct in Europe but found in fossil assemblages from the Pleistocene cold stages elsewhere in Eurasia (Sysoev and Schileyko, 2009; Horsák et al., 2010b; Hofmann et al., 2011).

Several species that were characteristic of Central Europe during the last full-glacial and Early Holocene but disappeared later are still common in the study area (Horsák et al., 2015). Thus, our study of snail composition in southern Siberian forest ecosystems can contribute to greater understanding of full-glacial boreal forests reconstructed for some areas of Central and Eastern Europe. These have been reconstructed based on fossil pollen and plant macrofossil records (Jankovská and Pokorný, 2008; Kuneš et al., 2008; Magyari et al., 2014) or projected by modelling (Janská et al., 2017). These reconstructions suggest existence of *Pinus*, *Picea* and *Larix*-dominated forests in topoclimatically favourable locations above the loess-steppe zone. In these areas, however, virtually no fossil data on land snails exist (except for two sites in Slovakia) due to acidic conditions hampering shell preservation. This makes any inferences about full-glacial forest land snail assemblages impossible. In contrast, precise information on the Pleistocene land snail assemblages of the loess zone (below ~400 m a.s.l.) exist across temperate Europe due to good shell preservation in loess accumulations (Ložek, 2001; Moine, 2014).

Here, using data from 173 natural forest sites distributed across a sharp climatic gradient in southern Siberia, we aim to identify the main predictors of snail species richness and abundance which could be compared with those reported from temperate Europe. We also describe the variation in snail diversity among the main forest types as potentially useful information for the reconstruction of European full-glacial forest snail fauna.

2. Material and methods

2.1. Data sampling

We collected data on land snail assemblages from 173 forest plots distributed across the main climatic gradient of the southern Siberian mountain systems, from the relatively warm and wet landscapes north of the Altai Mountains and in the Kuznetsk Alatau Mountains to the cold and dry landscapes in the south-eastern Russian Altai (Fig. 1). Forest vegetation along this gradient was described previously from the adjacent Western Sayan Mountains (Chytrý et al., 2008). The sites were selected to cover the entire range of natural forest ecosystems occurring in this area. We collected data in plots of 100 m^2 located within patches of homogeneous vegetation with a total cover of tree layer larger than 15%, avoiding strongly disturbed sites (e.g. recently logged, burned or heavily grazed forests). Sampling was done in June–August of 2005–2006, 2011–2012 and 2015. Larger species were searched by a single observer for 30–60 min per plot, focusing on all appropriate microhabitats. Small snails (< 5 mm in maximum dimension) were

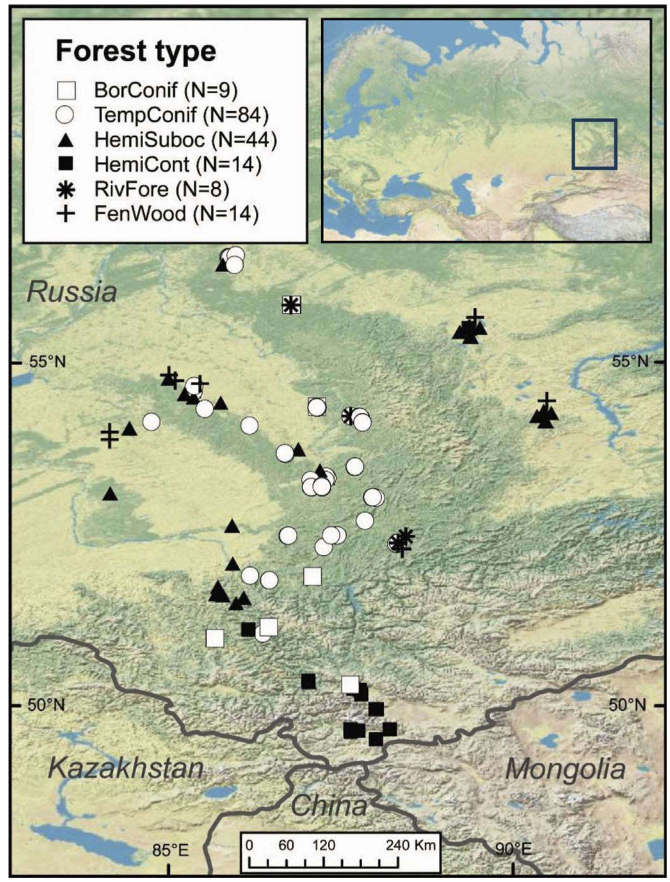

Fig. 1. Location of the study area and study sites classified into six main forest types. BorConif, Boreal coniferous forests; TempConif, Temperate coniferous and mixed forests; HemiSuboc, Hemiboreal suboceanic forests; HemiCont, Hemiboreal continental forests; RivFore, Riverine gallery forests; FenWood, Fen and swamp woodlands.

recorded by collecting 1–3litres of leaf litter, moss polsters and topsoil, depending on habitat heterogeneity. Litter samples from water-logged forests were wet sieved while dry litter was processed using standard protocols (Horsák et al., 2015). Snail taxonomy and nomenclature follow Sysoev and Schileyko (2009) and Nekola et al. (2015, 2018).

In each plot we also recorded species composition and cover of vascular plants in order to classify forest vegetation types. This classification was performed by an expert system prepared for this purpose based on similar principles as the expert system for European vegetation classes developed by Mucina et al. (2016). This expert system was based on comparing, within each plot, total square-rooted percentage covers of groups of species typical of the main phytosociological types of forest vegetation in this area as described by Ermakov et al. (2000) and Ermakov (2012). The classification by this expert system was run in the JUICE program (Tichý, 2002) and resulted in assignment of each plot to a single vegetation type. Similar vegetation types, especially those represented by few plots, were merged into six main forest types, the first four zonal and the last two azonal: (1) **Boreal coniferous forests** (n = 9), dominated by *Abies sibirica*, *Larix sibirica*, *Picea obovata* and *Pinus sibirica*, rich in ericoid dwarf shrubs (*Vaccinium* spp.), tall forbs, bryophytes and lichens, occurring in cool and wet areas, especially at higher altitudes; (2) **Temperate coniferous and mixed forests** (n = 84), also called *chernevaya* (blackish) taiga, dominated by *Abies sibirica, Betula* spp. and *Populus tremula*, rarely also by *Tilia sibirica*, and with admixture of *Padus avium, Picea obovata* and *Sorbus sibirica*, occurring in the warm and wet low-altitude areas in the northernmost Altai and in the lower mountains north of the Altai; (3) **Hemiboreal suboceanic forests** (n = 44), dominated by *Betula pendula* and *Pinus sylvestris*, locally also by *Populus tremula*, with a species-