Quaternary Science Reviews 93 (2014) 155–166

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Patterns of land-snail succession in Central Europe over the last 15,000 years: main changes along environmental, spatial and temporal gradients

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ARTICLE INFO

Article history:
Received 8 November 2013
Received in revised form
5 March 2014
Accepted 21 March 2014
Available online 8 May 2014

Keywords:
Central European refugia
Forest species
Holocene
Lateglacial
Mollusc succession
Palaeoenvironment reconstruction

ABSTRACT

Land snail shell assemblages have been used since the pioneering days of palaeoecology to describe Quaternary environmental changes. Despite the many advantages of this proxy, it has recently been rather overlooked. There are more than 300 mollusc successions from localities throughout the Czech and Slovak Republics, making this a globally unique archive. We selected 91 of these successions for radiocarbon dating and further detailed processing. Based on analyses of 828 mollusc assemblages we found a significant increase in both total species richness and number of forest species since the Lateglacial, with a decrease in both after the Middle Holocene. In contrast, the opposite response was found for open-country species and the proportion of xerophilous species. The proportion of forest and open-country species reversed at the Pleistocene/Holocene transition (approx. 11,500 cal yrs BP). Changes in species richness were rather stable across the study area and at different elevation, contrary to changes in species composition. MDS ordination based on presence/absence data show four main patterns of species composition associated with the number of forest species in a sample, position of site along the west–east direction, the proportion of hygrophilous species and, finally, with the age of the mollusc assemblage. The number of forest species indicates the main pattern of changes in the composition of Central European land snail assemblages from the Lateglacial to the present. We confirmed the application and temporal stability of ecological groups of snails as a useful tool for reconstruction of the terrestrial palaeoenvironment.

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1. Introduction

The geographical position of Central Europe, as a transitional zone between the oceanic and continental parts of Europe (Peel et al., 2007) and between the Alps and northern lowlands, affects the composition of many biotic assemblages, resulting in notably high regional species diversity (e.g. Cameron et al., 2010). During glacial periods, the mid-European zone between the Alpine and Continental glacial shields acted as a connecting line between eastern and western non-glaciated Europe. The resulting meeting of nearly all European faunal elements (e.g. Mediterranean, Atlantic, Siberian, Carpathian, Arctic and/or Alpine) is one of the most remarkable characteristics of the central European fauna, and many species have their western and eastern distributional borders in the region (for molluscs see Kerney et al., 1983; Welter-Schultes, 2012). Most of these species had already existed in this area since the beginning of the Middle Holocene, although some of them later retreated (Mania, 1995) while the spread of others is still occurring (Juřičková et al., 2013a). The modern distribution of many land snail species in the region is thus significantly influenced by their Holocene spread from traditional southern and/or recently discovered Central European (cryptic) refugia (for a review see Schmitt and Varga, 2012; refugia for snails discussed in Pfenninger et al., 2003; Pinceel et al., 2005; Ložek, 2006; Dépraz et al., 2008). Some forest species characteristic of interglacial periods survived the Last Glacial Maximum in the Western Carpathians, as recently supported by fossil data (Ložek, 2006; Jankovská and Pokorný, 2008; Juřičková et al., in press) as well as phylogeographical evidence (e.g. Kotlík et al., 2006; Magri et al., 2006; Magri, 2008). Broader evidence for a similar pattern of

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http://dx.doi.org/10.1016/j.quascirev.2014.03.019
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interglacial forest species surviving towards the western part of Central Europe is still lacking (Willis and van Andel, 2004), which implies another important, palaeobiogeographical border running through Central Europe (Kuneš et al., 2008). Thus, Central Europe, especially the area spanning from the Inner Western Carpathians towards the west of the Bohemian Uplands, is a crucial region for understanding Holocene distribution and spread of species throughout temperate Europe.

Land molluscs, especially shelled land snails, are one of the traditionally used proxies for palaeoenvironmental reconstructions, (e.g. Ložek, 1964, 2000; Sümegi, 2005; Davies, 2008) but have recently become been rather overlooked. Their shells are only preserved in calcareous rich environments, but in regions with calcium rich bedrock molluscs are usually the most abundant Quaternary fossils (e.g. Magnin, 1991; Preece, 1991; Ložek, 2000; Meyrick, 2001; Limondin-Lozouet and Preece, 2004), occurring in a wide range of sediments from dry steppe habitats to wetlands and also in a wide range of elevations (e.g. Mania, 1995; Ložek, 2000). There are two important advantages of snail fossils over other types of proxies for the reconstruction of Quaternary palaeoenvironments. Firstly, snail shells can be rather easily identified to species level, whereas plant pollen, probably the most commonly used palaeoecological proxy, is often identifiable only to genus or family (e.g. Moore et al., 1991). Secondly, unlike pollen or vertebrate remains, snail fossils are usually deposited directly in places where they lived, thus snail successions enable fine spatial resolution in the resulting palaeoenvironmental reconstruction. However, the latter can also be a disadvantage if only few successions are analysed, especially when attempting to generalize to the landscape level. If a representative network of sites is available (e.g. Ložek, 2001), however, this disadvantage can be overcome. Such networks of mollusc successions over Europe are still very sparse and uneven, partly as a result of the distribution of calcareous sediments necessary for shell fossilisation. While southern Britain has been studied in some detail (see reviews by Evans, 1972; Davies, 2008), data from most of the continent are scattered in many publications without any general conclusions. Central Europe has been the focus of intensive long-term research, resulting in several compendiums and hundreds of explored profiles providing the densest network of Holocene mollusc successions in the world (e.g. Mania, 1972, 1973, 1995;Fuhrmann, 1973; Alexandrowicz, 1987; Fükőh, 1993; Fükőh et al., 1995; Meyrick, 2001; Sümegi, 2005; Frank, 2006). Within Central Europe, the Czech Republic and Slovakia have provided a particularly rich archive of Holocene mollusc successions (the last summaries are published in Ložek, 1964, 1982a), with more than 300 sampled profiles (Horáčková et al., in press). Although empiric interpretations of this huge dataset were repeatedly published in the past (e.g. Ložek, 1964, 1982a, 1982b, 2000), no attempt has been made to explore spatial-temporal changes in this large dataset because many of the critical profiles lack secure chronologies underpinned by radiocarbon dating. To address this deficiency we selected a subset of the most important sites covering a broad range of different contexts for further analysis and dating.

In this study, we present a comprehensive analysis of 91 radiocarbon-dated mollusc successions from the Czech and Slovak Republics covering the last 15,000 years. We specifically seek to elucidate the main patterns of species richness and compositional changes since the Lateglacial, as well as explore the link with the biogeographic boundary between continental and Atlantic Europe. On the basis of 828 mollusc assemblages found in samples of all lithologically distinct layers in each succession, we modelled changes in species richness within the main ecological groups of land snails to explore differences separating general and local development across elevation and geographical position.

2. Material and methods

2.1. Sites and sampling

We selected 91 mollusc successions from 312 existing profiles across the Czech Republic and Slovakia (Horáčková et al., 2014) to cover as evenly as possible variations in time span, geographical distribution (from the Bohemian Uplands to the Western Carpathians), habitat diversity (floodplain, tufa, slope deposit, rock shelter, cave), and profile elevation (112–1550 m a.s.l.). Fig. 1 gives the position of these 91 profiles and the time-span of particular successions.

All these mollusc successions were sampled by standard methods (Ložek, 1964). 8 dm^3 of space discrete sediment samples (the top of one sample does not form the base of the next) were taken from the central part of each lithologically distinguishable layer within an 80 cm wide excavation pit, because the change of lithology means the change of habitat characters. We sampled all material in every lithological unit up to 8 dm^3 volume except for transitional zones between two lithologically distinct layers, which might be very sharp (samples nearly in contact) or rather thin (samples are few centimetres distant). Mollusc shells were extracted from the sediments by a combination of floating and sieving. After careful drying, each sample was disaggregated in water and if necessary in hydrogen peroxide. Floating shells and their fragments were repeatedly decanted into a 0.5 mm sieve and dried under laboratory conditions. Afterwards, the fraction retained by the sieve was dried and sorted by sieving into a variable number of fractions based on the type of resulting sediment. Shells were systematically removed from the sediment and identified under a dissection microscope. Molluscs were determined according to Ložek (1964) and L. Juřičková's and V. Ložek's personal comparative collections of recent and fossil shells.

Mollusc assemblages of particular layers frequently consist of species from several habitat types. This is mostly because fossiliferous localities are often situated in transitional habitats or at boundaries between them. For example, assemblages from cave entrances often consist of molluscs from the surrounding forest, as well as those from the rock wall above the entrance and steppe species that occur on the slopes above the cave.

2.2. Ecological groups

Ecological groups were applied *sensu* Ložek (1964, 1965). These groups were established based on i) detailed knowledge of the ecology of recent populations, ii) the changes in species occurrence during the whole Quaternary Climatic cycle. They reflect the situation within the region of Central Europe, and thus may differ in other parts of the continent. This classification results in ten main groups, first hierarchically dividing species into either terrestrial or aquatic, then terrestrial species into woodland, open-country or indifferent, and these three groups then divided into several subclasses based on humidity requirements. Aquatic species are also divided into several subgroups, but in this study we analysed only terrestrial species, since they are the most taxonomically and ecologically diversified groups of continental molluscs. In addition, aquatic species occurred only accidentally in the studied profiles, as these covered mainly terrestrial successions. The final classification of terrestrial snails contains the following nine groups of species that mostly inhabit: 1 – woodlands (*sensu stricto*); 2 – woodlands and also partly semi-opened habitats; 3 – damp and alluvial woodlands; 4 – xeric open habitats; 5 – open habitats in general (from moist meadows to steppes); 6 – various predominantly dry habitats; 7 – mesic or other various habitats (the group typically includes generalists and also synanthropic species); 8 –

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