Colonisation dynamic and diversity patterns of Holocene forest snail fauna across temperate Europe: The imprint of palaeoclimate changes

Michal Horsák, Nicole Limondin-Lozouet, Salomé Granai, Julie Dabkowski, Jan Divíšek, Petra Hájková

HAL Id: hal-02867878
https://hal.science/hal-02867878

Submitted on 5 Nov 2020

Colonisation dynamic and diversity patterns of holocene forest snail fauna across temperate Europe: The imprint of palaeoclimate changes

Michal Horsák [a,*], Nicole Limondin-Lozouet [b], Salome Granai [b,c], Julie Dabkowski [b], Jan Divíšek [a,d], Petra Hájková [a,e]

[a] *Department of Botany and Zoology, Masaryk University, Kotlářská 2, Brno, 611 37, Czech Republic*
[b] *CNRS, Université Paris 1, UPEC, UMR 8591, Laboratoire de Géographie Physique, 1 Place Aristide Briand, 92195, Meudon Cedex, France*
[c] *GéoArchéon, 30 rue de la Victoire, Viéville-sous-les-Côtes, 55210, France*
[d] *Department of Geography, Masaryk University, Kotlářská 2, Brno, 611 37, Czech Republic*
[e] *Laboratory of Paleoecology, Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, Brno, 602 00, Czech Republic*

ARTICLE INFO

ABSTRACT

The development of biotic communities since the last glaciation has been shaped by both dramatic climate changes and pathways of species colonisation from glacial refugia. Although the growing body of literature has emerged recently on possible scenarios of postglacial colonisation, less is known about the effect of climate. We analysed the dynamics of Holocene mollusc succession with an undetected human impact using three well-dated sequences from spring tufa deposits across temperate Europe. For the first time, the detailed Holocene mollusc successions can be compared with climate parameters in the corresponding time windows. High-resolution palaeoclimate data accompanied the species data, and the data derived from stable isotope analyses. The number of close-canopy forest species that colonised the sites until 5000 cal BP and the maximum number of species per sample systematically increased towards the interior of the continent. We also observed earlier colonisation of forest snail species in the Western Carpathians. While the aridity index was the best predictor of local species richness in Normandy and Luxembourg, minimum January temperature drove the variation in snail data in Slovakia. The short period of an abrupt cooling and drying around 8500 cal BP was found to stop the colonisation, sharply reducing the number of local species across the continent. Our results document the importance of climate for the colonisation and development of forest biota during the first half of the Holocene, both at continental and local scales. They also elucidate processes shaping the current distribution of forest snail fauna across the European temperate zone.

© 2020

1. Introduction

Climate changes have driven the development of Holocene communities and biodiversity patterns since the end of the last glaciation (e.g. Kuosmanen et al., 2016; Marquer et al., 2017). Likewise, the position of glacial refugia has influenced the colonisation pathways, mainly of cold-sensitive species (Stewart and Lister, 2001). These two factors played a crucial role especially in the first half of the Holocene when human impact by Mesolithic hunter-gatherers was mostly limited to local scales (Behre, 1988; Marquer et al., 2017). Changes of biotic communities at that time were thus influenced by climate warming and moistening once the ice sheets have started to melt. These climate changes triggered a massive and complex reorganisation of biotic communities with cold-adapted, stress-tolerant and competitively week species, being replaced by cold-sensitive species of nutrient-rich habitats (e.g. Birks, 1989; Miller et al., 2008). Their colonisation and expansion were for a long time believed to take place mainly from southern macrorefugia (e.g. Bennett et al., 1991). However, a still-growing body of literature provides the evidence for scattered local microrefugia of high importance for the recolonisation, constituting complex and mostly species-specific colonisation scenarios (e.g. Stewart et al., 2010; Schmitt and Varga, 2012).

For forest land snails, however, there was likely a more directional colonisation pattern of the Holocene range expansions (Hausdorf and Hennig, 2003) as the majority of European temperate snails probably had their glacial refugia eastwards in the Carpathian Mountains, which remained relatively forested during the Last Glacial (Ložek, 2006; Jankovská and Pokorný, 2008; Juřičková et al., 2014a). Because

forest species dominate contemporary land snail fauna of temperate Europe (Ložek, 1964; Juřičková et al., 2014b), understanding their Holocene dynamic and succession is of prime importance to explain their modern diversity and distributional patterns. The colonisation patterns and the continuity of forest snail faunas are also associated with the succession and changes in vegetation. The occurrence of many forest snails is closely related to the tree and herb layer composition and also to forest structure (e.g. Wäreborn, 1969; Kappes et al., 2009; Horsák et al., 2010). It is because only some trees (e.g. *Tilia, Fraxinus* and *Acer*) contain leaf litter calcium in a physiologically available citrate form, while many others (e.g. *Quercus, Carpinus* and *Fagus*) have an oxalate form, which is hard to utilise by snails (Wäreborn, 1969). Coniferous trees are unfavourable in general, but conditions in the forest floor can be improved by some broad-leaved herbs (e.g. Horsák et al., 2010). Many forest snails also rely on the deadwood of appropriate quality and amount, providing shelters in cold and dry periods (Kappes et al., 2009). Sparse forests are in general less diverse than those of closed canopy, which are also of high and stable humidity in their litter (Wäreborn, 1970; Bishop, 1976). The interaction of large scale and local scale processes thus shapes the succession of local snail assemblages.

There is rich literature on local Holocene land snail successions across temperate Europe (e.g. Ložek, 1964; Preece and Day, 1994; Meyrick, 2001; Limondin-Lozouet et al., 2013; Juřičková et al., 2014b; Horsák et al., 2019). Some studies also attempted to apply a multiproxy approach to reconstruct climate and vegetation changes in association with local land snail successions (e.g. Preece and Bridgland, 1999; Hájková et al., 2012; Granai and Limondin-Lozouet, 2018; Juřičková et al., 2018). Only recently, advanced climatic models have provided an accessible reconstruction of palaeoclimate continuously spanning the last 21,000 years at high temporal resolution (Fordham et al., 2017). It creates a unique opportunity to explore the colonisation patterns considering both local processes and macroclimate. We can also assess changes in mesoclimate using the stable isotope analysis of calcium carbonate-rich deposits, allowing for the reconstruction of local changes in temperature and rainfall amount (e.g. Andrews, 2006). As the preservation of mollusc shells requires a high amount of calcium in the soil (Ložek, 1964), some archives, such as tufa forming springs, provide a unique opportunity to combine the reconstruction based on snails and stable isotopes in tufa calcite (e.g. Andrews, 2006; Dabkowski, 2014; Juřičková et al., 2018).

In this regard, we assembled three, to our best knowledge, most detailed and complete Holocene land snail successions across a longitudinal transect from Western to Eastern temperate Europe. Our previous study showed a clear signal of eastern refugia for the majority of forest snail species in the study region (Horsák et al., 2019). This pattern is visible on the contemporary assemblages that are systematically depauperate in forest species from east to west (Kerney et al., 1983; Hausdorf and Hennig, 2003). However, it is still challenging to disentangle the relative importance of climate and/or vegetation changes from human modifications of the ecosystems for shaping the species distribution patterns. At large spatial scales, human pressure on natural forest communities became the main driver of their dynamic since the second half of the Holocene (e.g. Fyfe et al., 2015). Therefore to explore colonisation dynamic before the widespread development of agricultural landscapes during the Bronze Age, from ca. 4000 cal BP, it is essential to understand the importance of natural processes for the development of forest ecosystems and malacofauna. Some local studies suggest that the colonisation by forest species was rather slow, and might have therefore been blocked by the early human settlement in some areas (e.g. Ložek, 2011; Juřičková et al., 2013). Because it is challenging to separate these two processes, especially if they happened at the same time and locations, we selected only sites without any apparent human impact, both at the site and the surroundings (see below).

In this study, we analysed three well-dated Holocene land snail successions across temperate Europe and related them to new palaeoclimate data and stable isotopes from tufa sediment of fine resolution. The primary goal was to detect general and site-specific trends in the colonisation and succession dynamics of forest land snail faunas across temperate Europe. We explicitly seek to what extent palaeoclimate changes shaped these trends, and discuss possible effects of the distance from glacial refugia and local processes, such as vegetation succession, on the patterns of forest snail diversity. We aim to disentangle these factors using the data spanning from the Atlantic coast, the area poor in contemporaneous forest snail fauna, to the West Carpathian Mountains, hosting ca. twice as much forest snail species.

2. Material and methods

2.1. Selection of study successions

We selected three Holocene successions to explore in detail the development of Holocene forest land snail assemblages along a longitudinal transect across temperate Europe. The transect reflects the distance to the main glacial refugia of temperate European forest snail fauna that were located towards the east of Europe (see Horsák et al., 2019 for more literature). One of the consequences is the highly depauperate forest fauna in Atlantic Europe (Kerney et al., 1983; Limondin-Lozouet and Preece, 2014). The studied successions are the best candidates to explore the land snail fauna development, in relation to colonisation dynamics and climate changes, from several reasons: 1) All three deposits represent the same sedimentological environment, i.e. spring tufa. Apart from the fact that it is the only sedimentological environment that is both rich in forest land snail shells and can continuously capture the entire Holocene, the tufa has several advantages in itself. First, because of the high content of calcium carbonate, the environment not only favours the development of diverse mollusc assemblages but also provides excellent conditions for shell preservation (the latter is required for reliable identification to the species level). Second, it is a low energy environment (Limondin-Lozouet and Preece, 2014), thus providing a fine resolution of in situ preserved material (see Frodlová et al., 2018). By contrast, for example, colluvial deposits, commonly used in Central Europe (Ložek, 1964; Juřičková et al., 2014b), can either accumulate from a large area or be reworked. Third, as tufa sediments mainly contain calcite (sometimes even >95% CaCO$_3$), they are highly suitable for stable isotope (δ^{18}O and δ^{13}C) studies, from which palaeoclimatic conditions can be inferred (e.g. Andrews, 2006; Dabkowski, 2014). Last but not least, tufa also preserves other proxies such as plant macrofossils, vertebrate remains, insects, and sometimes pollen, allowing for multiproxy reconstructions (e.g. Dabkowski, 2014; Hájek et al., 2016). 2) Tufa deposits typically contain rich material in terms of shell counts (see Frodlová et al., 2018) which reduces a potential bias of variable sample size (see Palmer et al., 2000) as much as possible, thus enabling a direct comparison of the changes in species richness. 3) The selected successions allow for a reliable radiocarbon dating. Exclusively for this study, some additional samples were dated when necessary for the construction of a reliable depth-age model. Having a precise age of each sample, we could directly compare the diversity changes and fauna development among sites and relate these to the climatic events. It is the first time when detailed Holocene snail successions could be precisely compared in given time windows. 4) The successions cover the longest available time intervals of the Holocene out of any known successions from Atlantic Europe, West Continental Europe, and the West Carpathian Mts. Importantly, they also capture almost the entire part of the Early and Middle Holocene, i.e. the time intervals of the natural development of forest fauna and colonisation of species from glacial refugia (Ložek, 1964; Horsák et al., 2019). 5) All these sites represent undisturbed development of forest environment as no indication of open phases

during the forest development or human impacts during the Early and Middle Holocene periods have been detected (Limondin-Lozouet and Preece, 2004; Hájek et al., 2016; Granai et al., in press).

2.2. Brief description of study successions

The study sites are located along the west-to-east transect in temperate Europe (Fig. 1). Their location spans over the main climate and biogeographical regions of Europe defined by Olson et al. (2001) and the European Environmental Agency (EEA, 2002): Atlantic region (Saint-Germain-le-Vasson site in Normandy, northwest France; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet et al., 2005), Continental region (Direndall site in Luxembourg; Meyrick, 2000; Granai et al., in press), and Alpine region (Mituchovci site in Western Carpathians, southwest Slovakia; Hájek et al., 2016). Saint-Germain-le-Vasson tufa sequence (hereafter referred to as Saint Germain) is located about 15 km south of Caen near the village of Saint Germain-le-Vasson (48.9886° N, 0.3169° W). The tufa exposed in an old pit varies between 50 and 100 m in width and is 9.5 m thick. The onset of tufa formation occurred ca 10,800 cal BP and persisted until 4700 cal BP, thus covering the Early and Middle Holocene. The main body of the tufa is now dry, the source of the carbonate is probably the Calcaire de Caen (Middle Jurassic: Early to Middle Bathonian), the immediate bedrock is composed of sandstone schists; for more details see Limondin-Lozouet and Preece (2004). Direndall tufa sequence is located near the village of Lorentzweiler, on the eastern valley slope of the Mamer River (49.6853° N, 6.0911° E). The tufa body is ca 95 m long and ca 25 m wide. The carbonated sequence lies on Late-Glacial fluvial deposits developed above the geological bedrock (Elvingen Marls). It is 8.7 m thick and began to form ca 10,600 cal BP until at least 1800 cal BP (for more details see Dabkowski et al., 2015 and Granai et al., in press). Mituchovci tufa sequence is located close to the Horná Súča village (48.9459° N, 17.9733° E). It has developed on a small, still active, spring of a shallow circulation. The entire deposit depth (2.74 m) was sampled down to the bottom clay layer overlaying the flysch bedrock; for more details see Hájek et al. (2016) and Frodlová et al. (2018). Peat sediment rich in tufa has continuously accumulated since the very beginning of the Holocene (ca 11,600 cal BP) until present (Hájek et al., 2016).

2.3. Snail analyses and data harmonization

Shells were extracted using a standard protocol (Ložek, 1964): for details about each sequence processing see Limondin-Lozouet and Preece (2004): Saint Germain; Granai et al. (in press): Direndall; Frodlová et al. (2017): Mituchovci. Species were identified according to the same literature sources (Kerney et al., 1983; Horsák et al., 2013) and then the number of shells of each species in each layer was counted. For Saint Germain and Direndall sequences, some of the original layers were merged to reach at least 100 shells per sample in order to reduce the sampling artefact (see Frodlová et al., 2018). However, a few layers with <100 shells, but always >50, were used in the cases when there were clear changes in the species composition between the layers, or when the merging of these layers would exceed the accumulation time above 500 years. In all sequences, 80% of the analysed samples contained >120 shells and have accumulated for <400 years (Fig. 2).

2.4. Stable isotope analyses

Isotopic ratios of carbon and oxygen are directly associated with the malacological records of all three sites as the calcite samples composing the tufa sediment are those in which the shells were preserved. They thus provide strictly independent but perfectly synchronous data. Isotopes from Direndall and Mituchovci were measured at the *Service de Spectrométrie de Masse Isotopique* of the National Museum of Natural History in Paris (France) and those from Saint Germain at the *Stable Isotope Laboratory* of the University of East Anglia in Norwich (UK) following very similar protocols described in detail by Dabkowski (2011) and Dabkowski et al. (2015, 2019). In all cases, data reproducibility has been tested, and the replication of our own laboratory standards allowed to constrain confidence intervals (Table 1).

Fig. 1. Location of the three analysed sequences of Holocene forest snail successions. Satellite-derived land cover data were downloaded from https://www.naturalearthdata.com. Dark shade refers to forested and light to open landscape. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
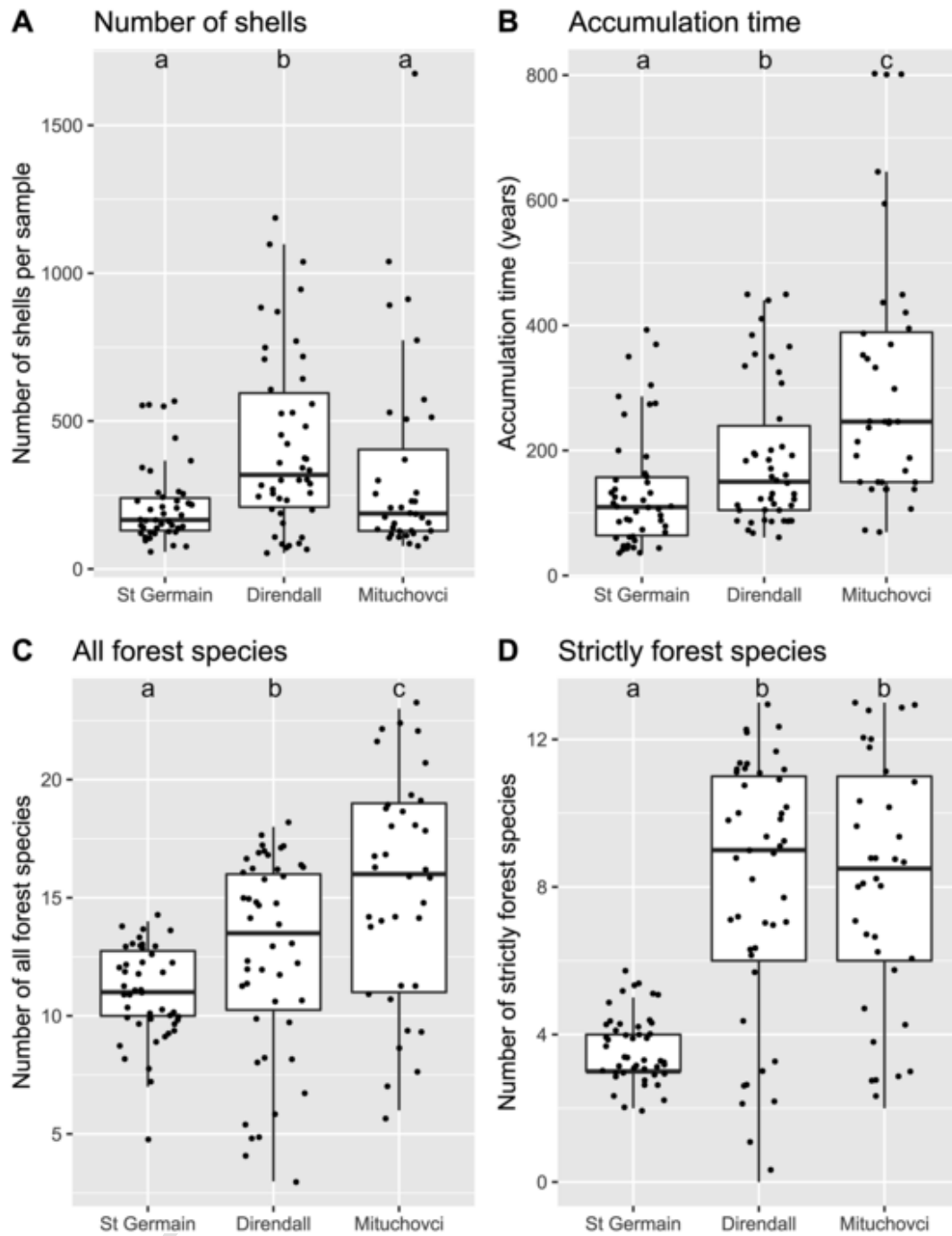
Fig. 2. Variation in the number of recorded land-snail shells, accumulation time and species richness for samples in the three studied mollusc sequences: Saint Germain, Direndall and Mituchovci. Dots show individual values. The central line of each box refers to the median value, box height to the interquartile range, whiskers to the non-outlier range (i.e. 1.5 times the interquartile range at each side), and dots outside of the range of whiskers to outliers. Significance of differences (at p < 0.05) among sequences, based on Kruskal-Wallis test and post-hoc Dunn test, are shown by small letters.

2.5. Radiocarbon dating and depth-age modelling

The depth-age model was created for each site in OxCal 4.2 (Bronk Ramsey, 2009) based on 6 (Saint Germain), 13 (Direndall) and 10 (Mituchovci) radiocarbon dates calibrated by using IntCal 13 calibration curve (Reimer et al., 2013). The models for Mituchovci and Direndall have already been published, for details see Hájek et al. (2016) and Granai et al. (in press). The model for Saint Germain was newly constructed using the same approach as for the Mituchovci and

Direndall, though it is mostly based on dates presented in Limondin-Lozouet and Preece (2004). Details on all dates and models are presented in Supplementary material (Table S1 and Fig. S1). On the basis of a P_Sequence function with the k parameter equal to 0.8 cm^{-1} (Mituchovci) and 1 cm^{-1} (Direndall and Saint Germain), the depth-age models with a 0.5-cm resolution were created. The command Boundary was applied when incorporating potential changes in the sedimentation rate, such as sediment transitions, into the models. The reason for this is the assumption that as the type of sediment changes, the sedimentation rate changes as well and thus the depth-age curve should change

Table 1
Summary of stable isotope data measured in samples (n) from the three studied sequences. For full data and details see Dabkowski (2011) for Saint Germain, Dabkowski et al. (2015) for Direndall, and Dabkowski et al. (2019) for Mituchovci.

		Saint Germain (n = 63)	Direndall (n = 118)	Mituchovci (n = 50)
δ ^{13}C (‰)	Mean	−9.3	−8.8	−8.13
	Range	−10.5/−7.9	−10.13/−7.75	−9.00/−6.49
	Conf. interval	±0.5	±0.04	±0.04
	Standart dev.	0.6	0.52	0.32
δ ^{18}O (‰)	Mean	−5.2	−6.30	−7.89
	Range	−5.2/−4.3	−6.74/−5.81	−8.58/−7.18
	Conf. interval	±0.2	±0.08	±0.09
	Standart dev.	0.2	0.16	0.52

its inclination. Putting a boundary in such locations in a depth-age model considers expected changes in sedimentation rate.

2.6. Palaeoclimate data preparation

We used PaleoView software (version 1.1.; Fordham et al., 2017) to generate monthly minimum, mean, and maximum temperatures (°C) and monthly rainfall amounts (mm/month) for continuous-time windows spanning 100 years from 11,500 to 500 cal BP. Climatic data provided by PaleoView came from the TRaCE21ka experiment (Liu et al., 2009), which uses the Community Climate System Model ver. 3 (CCSM3; Collins et al., 2006), a global coupled atmosphere-ocean-sea ice-land general circulation model. The data were generated for the whole of Europe in the form of raster files at a resolution of 2.5°. For a better reconstruction of palaeoclimate at studied sites, we downscaled the above-mentioned climatic variables to the spatial resolution of ~1 km using the delta-change method (Ramirez Villejas and Jarvis, 2010). This method relies on the calculation of absolute (for temperatures) or relative (rainfall) differences (anomalies) between baseline climatic data, representing observed climatic conditions in the period 1940–1989, and palaeoclimatic CCSM3 data corrected for model bias, i.e. for the difference between observed climate and model prediction for the same period. As baseline climatic data, we used monthly temperature and rainfall rasters obtained from the CHELSA database (Karger et al., 2017). Temperature and rainfall anomalies were then interpolated using multilevel B-spline interpolation and added (for temperatures) or multiplied (rainfall) to baseline climatic rasters. Monthly temperature and rainfall values were then extracted from downscaled raster data and assigned to the studied sites based on their spatial overlap.

To explain mollusc succession at each site, we used the minimum January temperature, maximum July temperature, annual, summer, and winter rainfall amounts, which were calculated based on downscaled monthly palaeoclimatic data described above. We also calculated Thornthwaite aridity index, which quantifies the degree of water deficit below water need (Thornthwaite, 1948). This index is based on monthly rainfall and potential evapotranspiration (PET) amounts. PET was derived from the downscaled monthly temperatures, and monthly extraterrestrial solar radiation, which was estimated for the midpoint of each time window using the 'palinsol' R package (Crucifix, 2016). Values of these climatic variables were assigned to each calibrated date using linear interpolation between the midpoints of time windows.

2.7. Statistical analyses

All graphics and analyses were conducted in the R software (R CoreTeam, 2018) with the packages 'rioja', 'vegan', 'ggplot2', 'ggpubr', 'stats', 'FSA, 'graphics', and 'PerformanceAnalytics', except for the changes of forest species illustrated in the C2 software (Juggins, 2007). Differences in the dependent and explanatory variables among the sequences were tested using a non-parametric Kruskal-Wallis rank sum test (due to not-normal distribution of most variables) and post-hoc Dunn test using adjusted p-values.

Spearman correlations were used to assess the relationships between all climatic and isotopic variables tested in this study as possible drivers of changes in forest snail species richness (Supplementary material, Fig. S2). To test the effect of these variables, we used multiple linear regression models as the numbers of forest species in all three sequences followed approximately normal distributions. Prior to the modelling, we drew Cleveland dot plots of all predictors and response variables to assess their distributions. Further, we assessed the shape of the relationships between response variables and predictors using pair plots. As there was an indication of possible quadratic responses for some variables (Supplementary material, Fig. S2), we also added quadratic term (marked as *^2) into the model and tested its significance. We added the mean calibrated age of each sample as another predictor because changes through time can covary with many variables and mechanisms, such as climate change, colonisation, vegetation succession, and change in the regional species pool. The importance of two variables, the number of shells and accumulation time, was also tested. These variables were included as they can represent potential bias because the number of species tends to increase with both the number of shells and accumulation time (see Frodlová et al., 2018).

We estimated the gross effect (expressed as adjusted R^2) and statistical significance (based on F statistics) of each of the ten predictors using a set of simple linear regression models. In the next step, we reran the models while controlling for potential bias caused by the effect of the number of shells and accumulation time. Finally, we constructed the most parsimonious multiple linear regression model for each site to find a set of uncorrelated significant predictors. As in the previous step, the number of shells and accumulation time entered the models first to test the effect of other variables on the residual variation. Then, the most influential variable based on the F statistic was added into the model, and the significance of its pure effect was tested using the F test. This procedure was repeated until all the predictors included in the model were significant at $p < 0.05$. For all final models presented in Table 2, we examined the patterns of residuals for fitted values and the values of individual predictors; we checked the residuals for normality and homogeneity of variance, and also explored influential observations using Cook's distance (Cook, 1977).

3. Results

In total, 5092, 6622, and 5036 snail shells were analysed in 46, 46, and 36 samples from Saint Germain, Direndall, and Mituchovci sequences yielding 21, 24, and 39 forest snail species, respectively (Table S2). The studied sequences differed in the number of shells analysed per sample (Fig. 2A), being statistically the same for Saint Germain and Mituchovci, but significantly higher for Direndall (p = 0.039). There were also differences in accumulation time (Fig. 2B), represented by longer intervals in Mituchovci, shorter in Direndall, and even shorter in Saint Germain, resulting in significant differences among all sequences (p < 0.013). While the number of all forest species significantly differed among all sequences (p < 0.019), increasing from Saint Germain to Mituchovci (Fig. 2C), there were no clear differences between Direndall and Mituchovci in strictly forest species (Fig. 2D). In

Table 2

Linear regression between the number of all forest land snail species and their potential determinants. Percentage value of adjusted explained variation (R^2) and its significance based on F statistic is expressed for: A, gross effects from regression models with a single predictor; B, pure effect of each predictor when both the variation explained by the number of shells (all sequences) and accumulation time (only for Mituchovci) were accounted for; C, the same as for B, but all significant variables in B sequentially entered the model (note that there was not any other significant predictor once the predictor with the highest explained variation entered the model). Signs in the brackets indicate the direction of response, either positive (+) or negative (−). Variables marked by "ˆ2" refer to models with a quadratic term included (the response was unimodal or asymptotical). Note that results for winter rainfall are not shown because no significant effect was found in any of the models.

No. of forest species	Saint Germain		Direndall		Mituchovci	
A: Gross effects	R^2 (%)	p	R^2 (%)	p	R^2 (%)	p
Calibrated age BP	–	n.s.	(−) 62.5	< 0.001	(−) 28.1	< 0.001
Calibrated age BPˆ2	29.2	< 0.001	76.0	< 0.001	46.5	< 0.001
January min. temp.	(+) 7.2	0.039	(+) 65.4	< 0.001	(+) 40.7	< 0.001
July max. temp.	–	n.s.	(−) 67.4	< 0.001	(+) 19.2	0.004
Annual rainfall	–	n.s.	(+) 61.5	< 0.001	(+) 23.7	0.002
Summer rainfall	–	n.s.	(+) 46.9	< 0.001	(+) 28.0	< 0.001
Summer rainfallˆ2	–	n.s.	51.8	< 0.001	–	n.s.
Aridity	–	n.s.	(−) 68.7	< 0.001	(−) 29.1	< 0.001
Aridityˆ2	30.8	< 0.001	–	n.s.	–	n.s.
δ^{18}O	–	n.s.	(−) 8.6	0.027	(+) 22.6	0.002
δ^{13}C	–	n.s.	(−) 54.1	< 0.001	–	n.s.
Number of shells	(+) 20.7	< 0.001	(+) 16.9	0.002	(+) 9.6	0.039
Acumulation time	–	n.s.	–	n.s.	(+) 16.1	0.009
B: Pure effects when no. of shells and accumulation time controlled						
Calibrated age BP	–	n.s.	(−) 65.6	< 0.001	(−) 26.4	< 0.001
Calibrated age BPˆ2	41.6	< 0.001	76.5	< 0.001	40.8	< 0.001
January min. temp.	–	n.s.	(+) 66.0	< 0.001	(+) 40.5	< 0.001
July max. temp.	–	n.s.	(−) 70.4	< 0.001	(−) 22.4	< 0.001
Annual rainfall	–	n.s.	(+) 66.4	< 0.001	(+) 36.8	< 0.001
Summer rainfall	–	n.s.	(+) 52.6	< 0.001	(+) 34.5	< 0.001
Aridity	–	n.s.	(−) 70.5	< 0.001	(−) 39.9	< 0.001
Aridityˆ2	41.3	< 0.001	–	n.s.	–	n.s.
δ^{13}C	–	n.s.	(−) 58.2	< 0.001	–	n.s.
δ^{18}O	–	n.s.	–	n.s.	(+) 19.5	0.01
C: Final model based on climatic variables; no. of shells and accumulation time controlled						
Aridity	–	–	(−) 70.5	< 0.001	–	–
Aridityˆ2	41.3	< 0.001	–	–	–	–

Table 2 (*Continued*)

No. of forest species	Saint Germain		Direndall		Mituchovci	
A: Gross effects	R^2 (%)	p	R^2 (%)	p	R^2 (%)	p
January min. temp.	–	–	–	–	(+) 40.5	< 0.001

contrast, notably and significantly lower numbers of strictly forest species appeared in samples from Saint Germain (p < 0.001).

The studied sequences significantly differed among each other (p < 0.05) in most of the climatic and isotopic variables (Fig. 3), increasing from Saint Germain to Mituchovci for summer rainfall and δ^{13}C or decreasing in the same order for minimum January temperature and δ^{18}O. Saint Germain and Mituchovci did not differ in annual rainfall, while Direndall received significantly higher rainfall (p < 0.001). In contrast, Direndall and Mituchovci did not differ in their aridity values, while Saint Germain was notably drier than the other two sequences (p < 0.001).

3.1. Tufa stable isotopes

A summary of isotopic data from Saint Germain, Direndall and Mituchovci is given in Table 1. Their distribution and comparison with other European sites are shown in Fig. 4. Both δ^{13}C and δ^{18}O values showed a clear trend with increasing continentality of the sites, consistent with those from European Late Quaternary tufas from the respective areas (Fig. 4). The decrease in δ^{18}O values from west to east is related to the well-known continental effect, while δ^{13}C values are typical of mid-latitude areas with strong soil-zone influence and where aridity/evaporation effects are low (i.e. with δ^{13}C values between −11 and −8‰). Clear differences appeared among the three sites in terms of the intra-site distribution of the isotopic values. Saint Germain and Direndall showed relatively large variations in δ^{13}C (SD = 0.6 and 0.52, respectively), while the variations in δ^{18}O were low (SD = 0.2 and 0.16, respectively) compared to Mituchovci, having more stable δ^{13}C (SD = 0.32), but highly variable δ^{18}O (SD = 0.52; Table 1 and Fig. 4).

3.2. Snail richness: changes through time and its drivers

In all studied sequences, we observed a unimodal relationship between the species richness and sample age (Fig. 5). The quadratic model explained significantly more variation in the species data than the linear model in all cases, being even insignificant for Saint Germain data (Table 2). The peak of forest snail diversity differed among the sequences, being observed already during the Early Holocene at Mituchovci and Saint Germain (Fig. 5). Virtually the highest and stable values (22 species) were reached already around 9200 cal BP at Mituchovci (note that a single sample at 5700 cal BP contained 23 spp.) and 8400 cal BP at Saint Germain. By contrast, the number of forest species at Direndall monotonically increased during the entire Mid-Holocene, peaking at ca 4700 cal BP (18 spp). This was mirrored by the amount of variation explained by age, being way higher for Direndall data (Table 2A). Both the number of shells per sample and accumulation time had significant effects on the number of species at Mituchovci, while only the number of shells was significant for the remaining two sequences. Once the data were controlled for the potential bias (Table 2B, C), changes in the species richness (pure effect) were best explained by minimum January temperature (40.5% of the total variance explained) at Mituchovci and by aridity index at Direndall (70.5%) and Saint Germain (41.3%).
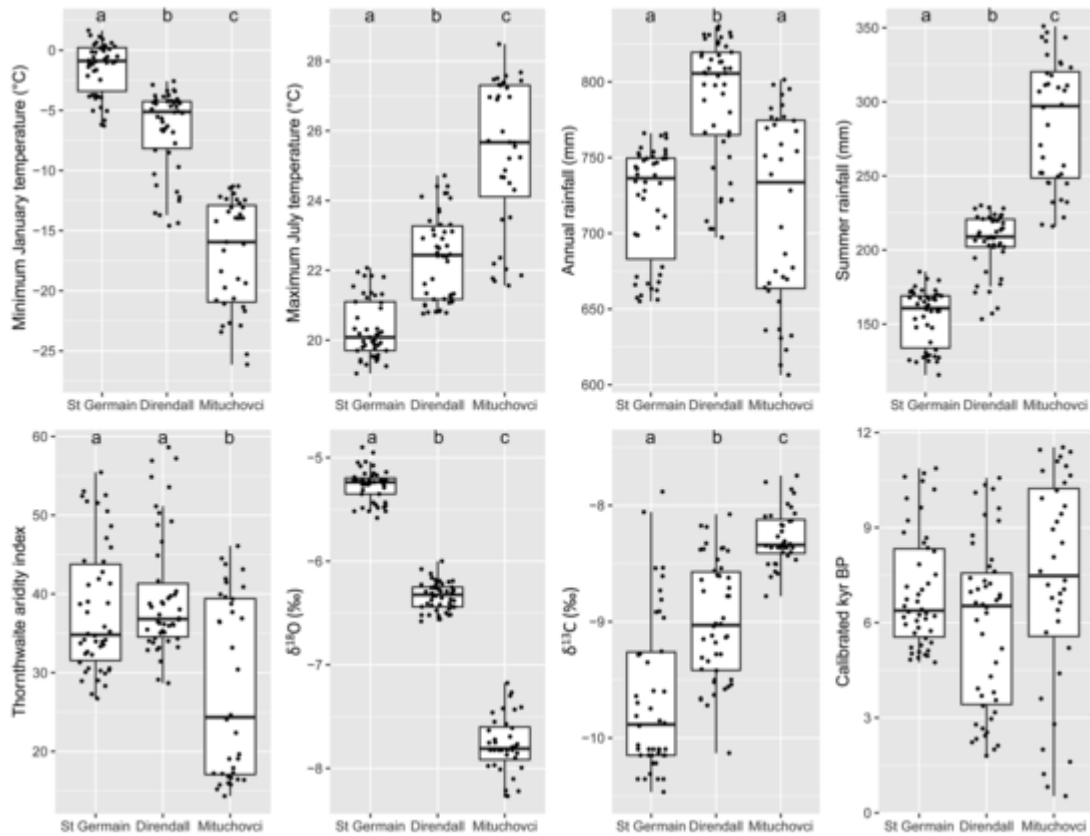
Fig. 3. Variation in values of climatic and isotopic variables for samples of the studied mollusc sequences: Saint Germain, Direndall and Mituchovci. For a description of boxplots and significance see Fig. 2.
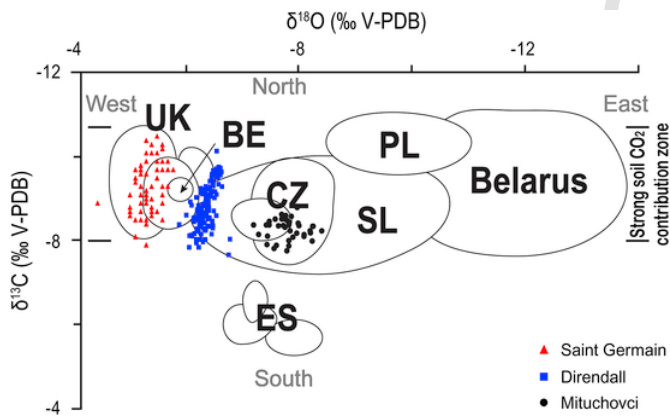

Fig. 4. Combined $\delta^{18}O$ and $\delta^{13}C$ plot for well-dated late Quaternary tufa calcites (modified after Andrews, 2006) as a framework of the isotopic distribution of tufa across Europe. The whole data from the three studied sites are plotted within this framework.

Fig. 5. Changes in the number of forest species recorded in samples of the three studied Holocene mollusc sequences. Grey areas represent 95% confidential interval of regression models (see Table 1).

3.3. Colonisation and extinction dynamics from west to east

In all sequences, a sharp increase in the species colonising the sites (i.e. the first colonisation wave) occurred towards the transition from Preboreal to Boreal periods (Fig. 6). The second colonisation wave appeared during the Boreal period but notably differed among the sequences in timing. It happened in the mid-Boreal, as early as 9800 cal BP at Mituchovci and around 9400 cal BP at Direndall, but close to the end of the Boreal around 8500 cal BP at Saint Germain. After these two colonisation waves, at least 70% of all forest species have had appeared at all sites before 8200 cal BP, i.e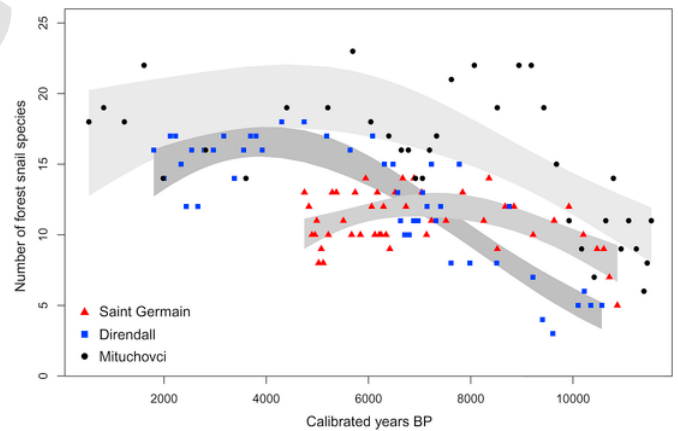. during the Early Holocene. At Saint Germain, with only two new species arriving during the Early Atlantic (around 8500 cal BP), the third colonisation wave happened mostly during the Late Atlantic. It was also the period of a distinct species turnover as seven species disappeared between ca 7200 and 5800 cal BP (Fig. 6). In contrast, the third wave happened during the second half of the Early Atlantic at Direndall, with 88% of all forest species in the sequence appearing before 7200 cal BP. At Mituchovci, the third wave was rather long and steady, taking place over the entire Atlantic period (ca 8000-4500 cal BP), with 25% of all forest species appearing during this period. Although there were virtually no local extinction events in Direndall, two and three clear periods of accelerated species extinction were found at Saint Germain and Mituchovci, respectively
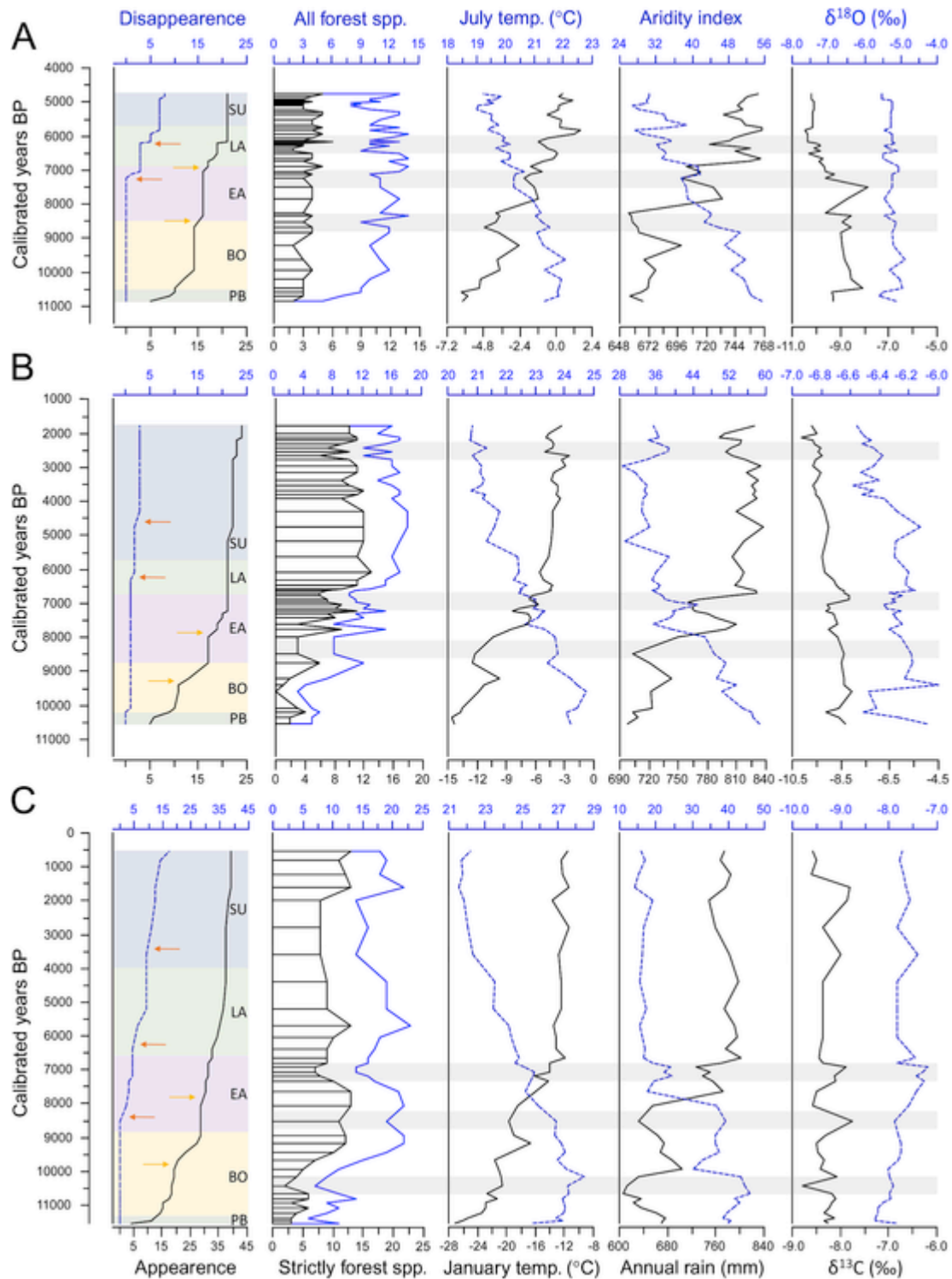
Fig. 6. Accumulation curves of local appearance and disappearance of all forest land snail species during the Holocene succession at the three studied sequences: A, Saint Germain; B, Direndall; C, Mituchovci; changes in numbers of strictly forest species (horizontal lines represent samples) and all forest species; and changes in selected climatic proxies (see Table 1). Orange arrows by solid lines show beginnings of colonisation waves after the first colonisation of the site since the Early Holocene. Red arrows by blue dash lines show the beginnings of notable extinction events or rapid species turnover. Main developmental stages of vegetation succession given in relation to classic Blytt–Sernander periods: PB, Preboreal; BO, Boreal; EA, Early Atlantic; LA, Late Atlantic; SU, Subboreal (and Subatlantic in case of Direndall and Mituchovci) are shown by colours. Saint Germain (adopted from Lespez et al., 2005 and Limondin-Lozouet et al., 2005): PB, early stage of forest development – *Pinus-Betula* ph.; BO, open canopy forest – *Corylus-Ulmus* ph.; EA-LA, mixed deciduous forest of middle Holocene – EA, *Tilia-Quercus* ph., LA, *Fagus-Quercus* ph.; SU, *Alnus-Fagus* ph. Direndall (adopted from Slotboom and Van Mourik, 2015): PB, early stage of forest development – *Pinus-Betula* ph.; BO, open canopy forest of – *Corylus-Quercus* ph.; EA-SU, expansion of mixed deciduous forests of middle and late Holocene (*Quercetum mixtum*) – EA, *Tilia-Quercus* ph., LA, *Fagus-Quercus* ph.; SU, local reduction of forests due to extension of agriculture – *Betula-Quercus* ph. Mituchovci (adopted from Hájek et al., 2016): PB, mosaic landscape of Pleistocene/Holocene transition – *Pinus-Picea* phase; BO, open canopy lime forest of Early Holocene – *Tilia-Ulmus* phase; EA-SU, mixed deciduous forest of middle and late Holocene (*Quercetum mixtum*) – EA, *Fraxinus-Hedera* ph., LA, *Tilia-Acer* ph., SU, *Fagus-uercus* ph. Pale-grey horizontal stripes mark arbitrarily selected stages of an abrupt decrease of species richness which seem to

concord with changes in climate. Note that δ18O data are normalised to a common mean value of zero to allow comparison between sites independently from variations due to the continental effect (see above). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Fig. 6). In all cases, they seemed to be associated with the changes in tree composition of the main vegetation biozones and climatic periods (Fig. 6).

3.4. Events of species richness reduction related to climate

In terms of the numbers of all forest species, a distinct longitudinal decrease from east to west was captured. However, this reduction was only about four or five species between the nearby sequences. In contrast, for strictly forest species, only three of them were recorded in the median sample at Saint Germain compared to nine species recorded at both Direndall and Mituchovci. The three periods of the reduced number of species at Saint Germain (i.e. 8500, 7200 and 6200 cal BP) seemed to be associated with the decrease of minimum January temperature and, especially for the two latter periods, with the decrease of annual rainfall (Fig. 6A). All these events also seemed to correlate with either the end of colonisation or the beginning of local extinction. Within Direndall data (Fig. 6B), at least three events of forest-species richness reduction at ca 8500, 6800 and 2500 cal BP seemed to be associated with minimum January temperature and annual rainfall in the first half of the Holocene, and probably aridity during the Subboreal. The first two climatic events are probably also responsible for the termination of colonisation waves. Three events of reduced species richness were also noticed in the Mituchovci record. They happened in the first half of the Holocene at ca 10,500, 8500 and 7000 cal BP (Fig. 6C) and were probably promoted by the decrease in rainfall and the increase in aridity. The notable decrease of minimum January temperature around 8500 cal BP seemed to terminate the first colonisation wave and trigger the first local extinction. Most of these events were also captured by local records of stable isotopes (Fig. 6).

4. Discussion

4.1. Climatic variation derived from stable isotopes

The inter-site variation of stable isotope data from Saint Germain, Direndall and Mituchovci chiefly reflects their geographical distribution along the west-east transect (Andrews, 2006). However, they differ in their patterns of intra-site variation of both δ13C and δ18O (Fig. 4). The complex interplay of processes that underlie these local variations is discussed in detail for each site by Dabkowski (2011) and Dabkowski et al. (2015, 2019). Regarding δ13C, in areas where the soil-zone effect dominates (conversely to aridity/evaporation effects; Fig. 4), wetter conditions increase the input of isotopically negative δ13C from soil and vegetation while the dissolution processes within the aquifer are reduced (see also Andrews, 2006). Conversely, a decreasing tufa calcite δ13C indicates increasing moisture. As the rainfall recharge decreases, the residence time of groundwater within the aquifer increases, resulting in a higher dissolution of carbonate with δ13C close to zero. The higher variation in δ13C values at Saint Germain and Direndall thus suggests higher moisture variation compared to Mituchovci. While little or no long-term variations seem to affect the Mituchovci record, the decrease of δ13C, reflecting increasing moisture, is observed at Saint Germain and Direndall, from 7500 cal BP and 6500 cal BP, respectively. This parallels the results of species richness modelling as the aridity index was the main predictor of changes in the number of all forest species recorded in samples from these sequences. The time lag observed at Saint Germain compared to Direndall may also explain a unimodal response at the former compared to a linear decrease at the latter. Tufa δ18O is mainly dependent on the isotopic composition of water from which calcite is precipitating, i.e. meteoric water that recharge groundwater-fed springs (Andrews et al., 1997; Janssen, 2000). Rainfall δ18O in temperate regions, at a given latitude

and altitude, is mainly controlled by air temperature changes (Dansgaard, 1964). Trends toward higher δ18O values in tufa calcite thus correspond to increasing air temperatures (Andrews et al., 1994, 2006). The low variation of δ18O values at Saint Germain and Direndall thus suggests relatively little temperature variation compared to Mituchovci. This is consistent with the observed principal role of temperature parameters on changes in the species richness at the Mituchovci site. The period of higher δ18O values at this site indicates a marked thermal maximum between 8500 cal BP and 6000 cal BP, which is also visible in the mollusc record as the number of strictly forest species is peaking between 8500 and 7500 cal BP.

4.2. Signal of the distance from glacial refugia of forest species

We found apparent differences among the studied sequences in the colonisation dynamic of forest species during the Early Holocene. While the numbers of forest snail species at the site (i.e. the regional species pool) sharply and continuously increased up to ca 9200 cal BP at Direndall and Mituchovci, no species arrived between ca 10,100 and 8600 cal BP at Saint Germain. Likewise, the uppermost values of local species richness increased from west to east, with 13–14, 17–18, and 22–23 forest species per sample at Saint Germain, Direndall, and Mituchovci, respectively. Even more contrasting differences were found based on the total number of all forest species that appeared until 4700 cal BP (i.e. the end of the shortest record). These numbers separated the two sites located towards the west, capturing a total of 21 (Saint Germain) and 22 (Direndall) forest species, from the easternmost located Mituchovci site with 36 species recorded over the same period. A comparable number of 30 forest species was recorded until 5400 cal BP at Valča site; another well-dated sequence from the Western Carpathians (Juřičková et al., 2018). Such a high species richness in the east can be explained by a weak impact of the previous glacial periods on the ecosystems. The persistence of forest patches and the existence of small refugial zones for forest biota in the Western Carpathians during the full glacial times are well documented (e.g. Brewer et al., 2002; Juřičková et al., 2014a; Magyari et al., 2014). The area harboured well-developed temperate broadleaf forests already in the first millennia of the Holocene (Hájek et al., 2016; Jamrichová et al., 2017). The difference between Western and Eastern Europe can also be promoted by landscape topography, as discussed by Horsák et al. (2019). Conversely, the westernmost European zone was in the periglacial area characterised by a frozen tundra environment, causing a dramatic obliteration of forest biota (Guiter et al., 2003; Moine, 2008). As a consequence, eastern series also benefit from more diversified forest land snail communities at the beginning of the Holocene (Frodlová et al., 2018). Juřičková et al. (2018) proposed that the Western Carpathians were probably an important source for the postglacial recolonisation of Central Europe by forest biota. This phenomenon can also be observed in the pattern of species colonisation at the Mituchovci site, as the accumulation curve reaches its final plateau as late as around 5000 cal BP. The further to the west, the longer was the distance from the main refugial areas. It restricted the pool of species only to those with either close refugia, or those with high dispersal capacity. Thus, the species accumulation curve reached its plateau notably earlier at Direndall (ca 7200 cal BP), before the period of a high human pressure on the landscape (Fyfe et al., 2015). At Saint Germain, the colonisation pattern was not continuous as suggested by two clear plateaus observed. The first one was reached already at 10,000 cal BP unless the two species arriving around 8500 cal BP are considered a separate colonisation event, and the final plateau appeared as late as around 6200 cal BP. Although the total number of

species was almost identical at Saint Germain and Direndall, the time course of the colonisation was very different, and it continued much longer at the former site than at the latter. Importantly, these differences running on the large spatial scale also explain differences observed at the local scale. While the maximum numbers of forest species exclusive for closed-canopy forests (hereafter called strictly forest species) were the same at Direndall and Mituchovci (maximum 13, median nine species), only six (median three) were recorded at Saint Germain. It can be explained not only by the distance to the closest refugia but also by long term climate settings. The high aridity in the first half of the Holocene and the overall lowest summer rainfall at Saint Germain, compared to the other two sequences, might have blocked new arrivals of strictly forest species and kept the number of species low and stable. The effect of climate was probably also strengthened by a decreasing forest density westwards (Fyfe et al., 2015). In contrast, during previous interglacial periods, reconstructed to be wetter than the Holocene, high numbers of strictly forest species of central European origin were documented from Western Europe (Limondin-Lozouet and Preece, 2014). Because the arrival of these strictly forest species was achieved by the end of the thermal optima, i.e. the initial interval of interglacial periods covered by our study, the leading role of climate over the human impact seems to be well supported.

4.3. Climate imprints in colonisation dynamic and local changes

The patterns of the colonisation dynamics discussed above can also be read as climatically-driven because the impact of climate is geographically organised (Davis et al., 2003). At the beginning of the Holocene, it can be argued that the position of refugia overdrived the importance of climate as a sharp increase of forest species was detected across the whole longitudinal extent in response to the rise of global temperatures (Renssen et al., 2009). The earlier thermal optimum towards the east of Europe (Davis et al., 2003; Hájková et al., 2016), along with the location of the Carpathian refugia, can also be related to the earlier maximum of local species richness around 9200 cal BP at Mituchovci. In contrast, the maximum value of species richness was approached much later at Direndall, not before 8000 cal BP. Such evaluation does not make much sense for Saint Germain as the numbers of both all forest and strictly forest species in samples did not show any trends. This pattern can, however, be related to the delayed colonisation by forest species, because the second colonisation wave started after 7000 cal BP and overlapped with the local disappearance of some species. Although the total number of species that managed to colonise the site until 5000 cal BP was similar to that at Direndall, the number of species available in the regional pool was always lower at Saint Germain. Between 7000 and 5000 cal BP, there were always 19–20 forest species in each sample at Direndall versus only 14–16 species at Saint Germain. Additionally, the size of the species pool has not changed since ca 10,000 cal BP at Saint Germain, in contrast to Direndall reaching its stable size at 7500 cal BP.

We identify several possible events of climate deterioration, potentially restricting both the land snail colonisation and species richness once the local species pool has been stabilised (i.e. colonisation and extinction events were in an equilibrium). Most of these events seem to correspond to the reduction of moisture (i.e. decrease of rainfall and/ or increase of aridity). For one or two of these events, it seems that climate cooling was also involved, which looks plausible, especially during the Early Holocene. In all sequences, a dropdown of species richness as well as species colonisation was recorded around 8500 cal BP. At Saint Germain, this episode was short as the number of species dropped down from 12 to 9 species between 8650 cal BP and 8500 cal BP, and raised back to 14 at 8350 cal BP. At Direndall, this period lasted for ca 800 years; a sharp increase in the number of newly appearing species was interrupted, and the colonisation was restored once

the climate improved. At Mituchovci, the effect on local species richness was rather small, but the period of cooler and drier climate, occurring abruptly after a steep increase in moisture and rainfall (Dabkowski et al., 2019), completely overlapped with the pause in species colonisation, showing the same pattern as that for Direndall. It seems that this climatic event has impacted the development of forest biota at the continental scale, from oceanic to more continental areas, and from areas far from forest refugia to those located in their close proximity. This event might seem to be associated with the event 8.2. However, the climate model clearly shows that it started earlier around 8700 cal BP. The plausibility of the model is confirmed by the isotope data and also by the mollusc records as mentioned above. This period of notably colder and drier climate seemed to be shorted in Saint Germain, abruptly ending at 8200 cal BP in contrast to later and more continuous climate amelioration around ca 7800 cal BP for the two remaining sites located farther from the ocean. As described by Dabkowski et al. (2019) for Mituchovci, this change likely corresponds to the first, globally significant, Holocene rapid climate change event (RCC) of generally colder and drier climate across the Northern Hemisphere (Alley and Ágústsdóttir, 2005), occurring between 9000 and 8000 cal BP (Mayewski et al., 2004). This RCC is considered to be related to the distinct cooling recorded in Greenland ice cores and Northern Atlantic marine cores at 8200 cal BP (Bond et al., 1997). However, starting in fact from ca 8600 cal BP, this period of climate deterioration has been observed from locations around the world. It thus seems that it was caused by solar input fluctuation rather than by the abrupt freshwater pulse into the North Atlantic, recorded in the Greenland ice cores at 8200 cal BP (Rohling and Pälike, 2005). Contrary to this well-documented event, we have to be more careful with the interpretation of the other events observed in malacological records. It is not clear to which extent they are caused by local changes in spring activity, vegetation development or even taphonomy and sampling size artefacts. For Mituchovci, Dabkowski et al. (2019) suggested an explanation for the first cold event that appeared around 10,400 cal BP. It probably corresponds to the short cold event recorded across the Northern Hemisphere around 10,300 cal BP, in both Greenland ice cores and Northern Atlantic marine cores (Bond et al., 1997) and some continental European records (Bjo¨; rck et al., 2001; Starkel et al., 2013). The beginning of a short period with a reduced species diversity also appeared at Direndall around 10,100 cal BP and could be related to the same climatic event. This example suggests that it can be important to compare several geographically distributed profiles to seek for more general patterns in climate effects on Holocene biota development.

4.4. Disentangling the effect of climate and vegetation per se

Land snail distribution is, among other factors such as calcium content, strongly controlled by their sensitivity to low-temperature (e.g. Nicolai and Ansart, 2017) because these invertebrates cannot produce any cryoprotective chemicals (Riddle, 1983). However, the effect of temperature can be buffered by vegetation and leaf litter cover (Ansart et al., 2001; Horsák et al., 2013). Vegetation provides the main food resource as the majority of land snail species can be considered general grazers (Speiser, 2001). In some environments, vegetation may also represent the principal source of calcium for snail growth and reproduction (Wäreborn, 1969). Thus, climate changes can have both direct and indirect effects on the development of snail assemblages, with the latter being mediated through the succession of vegetation. To disentangle these two processes is not trivial, and the effect of vegetation per se should be taken into account when interpreting the changes related to climate. Our data suggest that the Holocene changes in vegetation mostly correlate with the increase of species turnover, triggering the colonisation of new species as well as the disappearance

of the others. The fast increase of species diversity in response to the rise of winter temperature was observed in all three sequences. This change, however, clearly corresponds with the colonisation of strictly forest snail taxa (i.e. snails restricted to closed-canopy forests). In Mitu-chovci (Hájek et al., 2016) and Saint Germain (Limondin-Lozouet et al., 2005) sequences, the associated pollen data indicate the shift of for-est vegetation from a *Picea-Pinus-Betula* dominated mosaic landscape of Preboreal vegetation type to Boreal type with *Tilia-Ulmus-Corylus* domi-nated forests. This succession change also represents the shift from tree taxa of unfavourable leaf litter chemistry towards the taxa favoured by land snails, with physiologically accessible citrate calcium in leaf litter (Wäreborn, 1969). However, this environmental shift occurred much earlier in Mituchovci (around 11,300 cal BP) while it was registered only at 10,300 cal BP in Saint Germain. In Direndall, the spread of for-est snail species also occurred at 10,300 cal BP, suggesting a similar chronology as that for Saint Germain. Because such a lag is not present in the temperature curve, as shown by palaeoclimate data, it seems that the malacological succession was mostly related to vegetation changes. Of course, also colonisation dynamic related to the position of forest refugia is part of this story (see above). At this stage of the Boreal period, more than half of all forest species recorded in each sequence have al-ready appeared. The transition to closed-canopy forests of the Early At-lantic coincides with the second colonisation wave of forest snails, hap-pening once the climate has ameliorated after the 8.5 cold event dis-cussed above. At Mituchovci, it was also associated with the local ex-tinction of *Discus ruderatus*, a cold-adapted species characteristic of the Early Holocene. At Direndall, this period was characterised by the ar-rival of many new species creating a regional species pool rich enough to cause a distinct increase of the species richness in the second half of this period. The forests of this period provided optimal conditions for snails due to the dominance of trees with favourable leaf litter chem-istry. The appearance and the optimum of *Tilia* tree in Luxembourg dur-ing the Early Atlantic (Slotboom and Van Mourik, 2015) may well explain the improvement of conditions for strictly forest snails at Diren-dall. In contrast, at Saint Germain, the second main colonisation wave was postponed to the Late Atlantic. In this period, however, the forest vegetation developed towards the dominance of beech and oak trees, which are producing generally unfavourable leaf litter for snails (Wäre-born, 1969). This assumption can be tracked down by the equilibrium between the colonisation and extinction events with some species (e.g. *Macrogastra rolphii*) appearing and also disappearing during this period. It seems that the time coincidence of snail spread from the refugia with the vegetation development was an important milestone for the local colonisation patterns of snail assembles.

5. Conclusions

The colonisation dynamic of forest land snails on the onset of the Holocene was shaped mainly by the increase in winter temperature and the vegetation shift from conifer-dominated to deciduous tree-domi-nated forests. The pattern of species colonisation was uniform across the continent, although it happened 1000 years earlier towards the east (ca 11,300 vs 10,500 cal BP). This time lag towards the west was probably related to the distance from the main glacial refugia of temperate for-est malacofauna, increasing towards the west. The second and the third colonisation waves were observed at a similar time for Luxemburg and Slovakia (around 9500 and 8000 cal BP for the second and the third wave, respectively), but they happened later in Normandy (ca 8500 and 7000 cal BP).

The proximity of glacial refugia, evidenced in the Western Carpathi-ans in Slovakia, seemed to affect also the total number of species colonis-ing each region in the first half of the Holocene. The total species pool is twice as large in Slovakia when compared with the remain-ing sequences located westwards. Although no difference in the

size of the species pool was found between the sequences from Luxem-burg and Normandy, the fewer number of strictly forest species man-aged to reach Normandy than Luxemburg. The numbers of forest species recorded in samples monotonically decreased from east to west. How-ever, the numbers of strictly forest species were similar in Luxembourg and Slovakia, but three times smaller in Normandy.

The variation in the number of forest species was explained mainly by minimum January temperature in Slovakia, but the value of aridity index was the best predictor in both westward located sequences. Cli-mate and related changes of the forest types seem to be the main factors affecting the succession of forest snails and their diversity at both local and regional scales. Several periods of climate deterioration, i.e. the pe-riods of cooler and drier climate, were recognized to have affected both snail colonisation and their local diversity. The short period of an abrupt climatic cooling and drying around 8500 cal BP was found to stop the colonisation of species for some time and also sharply reduce the num-ber of local species in all three sequences across temperate Europe.

The observed patterns of forest snail colonisation were captured at the sites with undetected human impact and over the first half of the Holocene, i.e. when human impacts at landscape level were in general negligible. Our observation suggests a leading role of the Holocene cli-mate on constituting the contemporaneous distribution of forest snail di-versity, sharply decreasing from east to west, with only a few strictly forest snail species occurring in Atlantic Europe.

Declaration of competing interest

The authors declare that they have no known competing for financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.quascirev.2020.106367.

Author statement

All authors should have made substantial contributions to a submis-sion. Their individual contribution is provided below and also in the manuscript. All authors have approved the revised version of the manu-script.

Authors contribution: MH conceived the idea, analysed the data and led the writing. NLL, SG and MH compiled snail data; PH constructed age-depth models; JDa prepared and analysed stable isotope data, and JDi prepared palaeoclimate data. All authors provided ecological inter-pretations of the results and participated in the manuscript preparation and writing.

References

Alley, R B, Ágústsdóttir, A M, 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. Quat. Sci. Rev. 24, 1123–1149.
Andrews, J E, 2006. Palaeoclimatic records from stable isotopes in riverine tufas: synthesis and review. Earth Sci. Rev. 75, 85–104.
Andrews, J E, Pedley, H M, Dennis, P F, 1994. Stable isotope record of palaeoclimatic change in a British Holocene tufa. Holocene 4, 349–355.

Andrews, J E, Riding, R, Dennis, P F, 1997. The stable isotope record of environmental and climatic signals in modern terrestrial microbial carbonates from Europe. Palaeogeogr. Palaeocl. 129, 171–189.

Ansart, A, Vernon, P, Daguzan, J, 2001. Photoperiod is the main cue that triggers supercooling ability in the land snail, Helix aspersa (Gastropoda: Helicidae). Cryobiology 42, 266–273.

Behre, K E, 1988. The role of man in European vegetation history. In: Huntley, B, Webb, T (Eds.), Vegetation History. Springer, Dordrecht, pp. 633–672.

Bennett, K D, Tzedakis, P C, Willis, K J, 1991. Quaternary refugia of north European trees. J. Biogeogr. 18, 103–115.

Birks, H J B, 1989. Holocene isochrones maps and patterns of tree-spreading in the British Isles. J. Biogeogr. 16, 503–540.

Bishop, M J, 1976. Woodland mollusca around nettlecombe, somerset. Field Stud. 4, 457–464.

Björck, S, Muscheler, R, Kromer, B, Andresen, C S, Heinemeier, J, Johnsen, S J, et al., 2001. High-resolution analyses of an early Holocene climate event may imply decreased solar forcing as an important climate trigger. Geology 29, 1107–1110.

Bond, G, Showers, W, Cheseby, M, Lotti, R, Almasi, P, Priore, P, et al., 1997. A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. Science 278, 1257–1266.

Brewer, S, Cheddadi, R, Beaulieu de, J L, Reille, M, 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period Data contributors. For. Ecol. Manag. 156, 27–48.

Bronk Ramsey, C, 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.

Collins, W D, Bitz, C M, Blackmon, M L, Bonan, G B, Bretherton, C S, Carton, J A, et al., 2006. The community climate system model version 3 (CCSM3). J. Clim. 19, 2122–2143.

Cook, R D, 1977. Detection of influential observations in linear regression. Technometrics 19, 15–18.

Crucifix, M, 2016. Palinsol: Insolation for Palaeoclimate Studies. R package version 0.93. https://CRAN.R-project.org/package=palinsol.

Dabkowski, J, 2011. Analyse géochimique des tufs calcaires en domaine fluviatile ouest européen: reconstitution de variations des paléotempératures et des paléoprécipitations au cours des interglaciaires des stades 11 et 5 PhD thesis. Muséum national d'Histoire naturelle, Paris, p. 303.

Dabkowski, J, 2014. High potential of calcareous tufa for integrative multidisciplinary studies and prospects for archaeology in Europe. J. Archaeol. Sci. 52, 72–83.

Dabkowski, J, Brou, L, Naton, H G, 2015. New stratigraphic and geochemical data on the Holocene environment and climate from a tufa deposit at Direndall (Mamer Valley, Luxembourg). Holocene 25, 1153–1164.

Dabkowski, J, Frodlová, J, Hájek, M, Hájková, P, Petr, L, Fiorillo, D, et al., 2019. The first whole-Holocene climate and environment record in the Western Carpathians derived from a tufaceous spring fen deposit (Slovakia). Holocene 29, 493–504.

Dansgaard, W, 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

Davis, B A S, Brewer, S, Stevenson, A C, Guiot, J, 2003. The temperature of Europe during the Holocene reconstructed from pollen data data contributors. Quat. Sci. Rev. 22, 1701–1716.

EEA, 2002. Europe's Biodiversity - Biogeographical Regions and Seas. https://www.eea.europa.eu/publications/report_2002_0524_154909.

Fordham, D A, Saltré, F, Haythorne, S, Wigley, T M, Otto-Bliesner, B L, Chan, K C, et al., 2017. PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. Ecography 40, 1348–1358.

Frodlová, J, Hájková, P, Horsák, M, 2018. Effect of sample size and resolution on palaeomalacological interpretation: a case study from Holocene calcareous-fen deposits. J. Quat. Sci. 33, 68–78.

Fyfe, R M, Woodbridge, J, Roberts, N, 2015. From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. Global Change Biol. 21, 1197–1212.

Granai, S, Limondin-Lozouet, N, 2018. The Holocene expansion of grassland in northern Europe reconstructed from molluscan assemblages. Boreas 47, 768–779.

Granai, S., Dabkowski, J., Hájková, P., Naton, H.-G., Brou, L., (in press). Holocene palaeoenvironments from the Direndall tufa (Luxembourg) reconstructed from the molluscan succession and stable isotope records. Holocene.

Guiter, F, Andrieu-Ponel, V, Beaulieu, J-L De, Cheddadi, R, Calvez, M, Ponel, P, et al., 2003. The last climatic cycles in Western Europe: a comparison between long continuous lacustrine sequences from France and other terrestrial records. Quat. Int. 111, 59–74.

Hájek, M, Dudová, L, Hájková, P, Roleček, J, Moutelíková, J, Jamrichová, E, et al., 2016. Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape. Quat. Sci. Rev. 133, 48–61.

Hájková, P, Horsák, M, Hájek, M, Lacina, A, Buchtová, H, Pelánková, B, 2012. Origin and contrasting succession pathways of the Western Carpathian calcareous fens revealed by plant and mollusc macrofossils. Boreas 41, 690–706.

Hájková, P, Pařil, P, Petr, L, Chattová, B, Grygar, T M, Heiri, O, 2016. A first chironomid-based summer temperature reconstruction (13-5 ka BP) around 49°N in inland Europe compared with local lake development. Quat. Sci. Rev. 141, 94–111.

Hausdorf, B, Hennig, C, 2003. Nestedness of northwest European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. Oecologia 135, 102–109.

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, Danihelka, J, Kočí, M, Kubešová, S, Lososová, et al., 2010. Snail faunas in the Southern Ural forests and their relations to vegetation: an analogue of the Early Holocene assemblages of Central Europe? J. Molluscan Stud. 76, 1–10.

Horsák, M, Limondin-Lozouet, N, Juřičková, L, Granai, S, Horáčková, J, Legentil, C, Ložek, V, 2019. Holocene succession patterns of land snails across temperate Europe: east to west variation related to glacial refugia, climate and human impact. Palaeogeogr. Palaeocl. 524, 13–24.

Jamrichová, E, Petr, L, Jiménez-Alfaro, B, Jankovská, V, Dudová, L, Pokorný, P, et al., 2017. Pollen-inferred millennial changes in landscape patterns at a major biogeographical interface within Europe. J. Biogeogr. 44, 2386–2397.

Jankovská, V, Pokorný, P, 2008. Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). Preslia 80, 307–324.

Janssen, A, 2000. Petrography and Geochemistry of Active and Fossil Tufa Deposits from Belgium. PhD thesis Katholieke Universiteit, Leuven, p. 392.

Juggins, S, 2007. C2 Version 1.5 User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation. Newcastle University, Newcastle upon Tyne, UK, p. 73.

Juřičková, L, Horáčková, J, Jansová, A, Ložek, V, 2013. Mollusc succession of a prehistoric settlement area during the Holocene: a case study of the České středohoří Mountains (Czech Republic). Holocene 23, 1811–1823.

Juřičková, L, Horáčková, J, Ložek, V, 2014. Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. Quat. Res. 82, 222–228.

Juřičková, 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.

Juřičková, L, Pokorný, P, Hošek, J, Horáčková, J, Květoň, J, Zahajská, et al., 2018. Early postglacial recolonization, refugial dynamics and the origin of a major biodiversity hotspot. A case study from the Malá Fatra Mountains, Western Carpathians, Slovakia. Holocene 28, 583–594.

Kappes, H, Jabin, M, Kulfan, J, Zach, P, Topp, W, 2009. Spatial patterns of litter-dwelling taxa in relation to the amounts of coarse woody debris in European temperate deciduous forests. For. Ecol. Manag. 257, 1255–1260.

Karger, D N, Conrad, O, Böhner, J, Kawohl, T, Kreft, H, Soria-Auza, R W, et al., 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 170122. doi:10.1038/sdata.2017.122.

Kerney, M P, Cameron, R A D, Jungbluth, J H, 1983. Die Landschnecken Nord- und Mitteleuropas. Verlag Paul Parey, Hamburg & Berlin.

Kuosmanen, N, Seppä, H, Alenius, T, Bradshaw, R H, Clear, J L, Filimonova, L, et al., 2016. Importance of climate, forest fires and human population size in the Holocene boreal forest composition change in northern Europe. Boreas 45, 688–702.

Lespez, L, Clet-Pellerin, M, Limondin-Lozouet, N, Pastre, J F, Fontugne, M, 2005. Discontinuités longitudinales des dynamiques sédimentaires holocènes des petites vallées de l'ouest du Bassin parisien, l'exemple de la Mue (Basse-Normandie). Quaternaire 16, 273–298.

Limondin-Lozouet, N, Preece, R C, 2004. Molluscan successions from the Holocene tufa of St-Germain-le-Vasson in Normandy, France. J. Quat. Sci. 19, 55–71.

Limondin-Lozouet, N, Gauthier, A, Preece, R C, 2005. Enregistrement des biocénoses de la première moitié de l'Holocène en contexte tufacé à Saint-Germain-le-Vasson (Calvados). Quaternaire 16, 255–271.

Limondin-Lozouet, N, Preece, R C, 2014. Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe. J. Molluscan Stud. 80, 224–237.

Limondin-Lozouet, N, Preece, R C, Antoine, P, 2013. The Holocene tufa at Daours (Somme valley, northern France): malacological succession and palaeohydrological implications. Boreas 42, 650–663.

Liu, Z, Otto-Bliesner, B L, He, F, Brady, E C, Tomas, R, Clark, P U, et al., 2009. Transient simulation of last deglaciation with a new mechanism for bolling–allerod warming. Science 325, 310–314.

Ložek, V, 1964. In: Quartärmollusken der Tschechoslowakei. Rozpravy Ústředního ústavu geologického, 31 (Praha).

Ložek, V, 2006. Last glacial paleoenvironments of the West Carpathians in the light of fossil malacofauna. Anthropozoikum 26, 73–84.

Ložek, V, 2011. Chronostratigrafic revision and paleoclimatic significance of the talus deposit at the foot of the Martinka cliff in the Protected landscape area and Biosphere reserve Pálava (South Moravia). Geoscience Research Reports for 44, 66–69 2010.

Magyari, E K, Kuneš, P, Jakab, G, Sümegi, P, Pelánková, B, Schäbitz, F, et al., 2014. Late Pleiglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? Quat. Sci. Rev. 95, 60–79.

Marquer, L, Gaillard, M J, Sugita, S, Poska, A, Trondman, A K, Mazier, F, et al., 2017. Quantifying the effects of land use and climate on Holocene vegetation in Europe. Quat. Sci. Rev. 171, 20–37.

Mayewski, P A, Rohling, E E, Stager, J C, Karlén, W, Maasch, K A, Meeker, L D, et al., 2004. Holocene climate variability. Quat. Res. 62, 243–255.

Meyrick, R A, 2000. Holocene molluscan faunal history and environmental change from a tufa at Direndall, Luxembourg. Bull. Soc. Préhist. Luxembourgeoise 22, 55–75.

Meyrick, R A, 2001. The development of terrestrial mollusc faunas in the "Rheinland" region (western Germany and Luxembourg) during the Lateglacial and Holocene. Quat. Sci. Rev. 20, 1667–1675.

Miller, P A, Giesecke, T, Hickler, T, Bradshaw, R H, Smith, B, Seppä, H, et al., 2008. Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia. J. Ecol. 96, 247–259.

Moine, O, 2008. West-European malacofauna from loess deposits of the Weichselian upper Pleniglacial: compilation and preliminary analysis of the Database. Quaternaire 19, 11–29.

Nicolai, A, Ansart, A, 2017. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. Conserv. Physiol. 5, ox007.

Olson, D M, Dinerstein, E, Wikramanayake, E D, Burgess, N D, Powell, G V, Underwood, E C, et al., 2001. Terrestrial Ecoregions of the World: a New Map of Life on Earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51, 933–938.

Palmer, M W, Clark, D A, Clark, D B, 2000. Is the number of tree species in small tropical forest plots nonrandom? Community Ecol. 1, 95–101.

Preece, R C, Bridgland, D R, 1999. Holywell coombe, folkestone: a 13,000 year history of an English chalkland valley. Quat. Sci. Rev. 18, 1075–1125.

Preece, R C, Day, S P, 1994. Comparison of Post-glacial molluscan and vegetational successions from a radiocarbon-dated tufa sequence in Oxforfshire. J. Biogeogr. 21, 463–478.

Ramirez Villejas, J, Jarvis, A, 2010. Downscaling Global Circulation Model Outputs: the Delta Method. Decision and Policy Analysis Working Paper No. 1. International Center for Tropical Agriculture (CIAT). Cali. CO, p. 18.

Reimer, P J, Bard, E, Bayliss, A, Beck, J W, Blackwell, P G, Ramsey, C B, et al., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887.

Renssen, H, Seppä, H, Heiri, O, Roche, D M, Goosse, H, Fichefet, T, 2009. The spatial and temporal complexity of the Holocene thermal maximum. Nat. Geosci. 2, 411–414.

Riddle, W A, 1983. Physiological ecology of snails and slugs. In: Russell-Hunter, W D (Ed.), The Mollusca. Volume 6: Ecology. Academic Press, New York, New York, USA, pp. 431–461.

Schmitt, T, Varga, Z, 2012. Extra-Mediterranean refugia: the rule and not the exception? Front. Zool. 9, 22.

Slotboom, R T, Van Mourik, J M, 2015. Pollen records of mardel deposits: the effects of climatic oscillations and land management on soil erosion in Gutland, Luxembourg. Catena 132, 72–88.

Speiser, B, 2001. Food and feeding behaviour. In: Barker, G M (Ed.), The Biology of Terrestrial Molluscs. CABI Publishing, Wallingford, pp. 259–288.

Starkel, L, Michczyńska, D, Krąpiec, M, Margielewski, W, Nalepka, D, Pazdur, A, 2013. Progress in the Holocene chrono-climatostratigraphy of polish territory. Geochronometria 40, 1–21.

Stewart, J R, Lister, A M, 2001. Cryptic northern refugia and the origins of the modern biota. Trends Ecol. Evol. 16, 608–613.

Stewart, J R, Lister, A M, Barnes, I, Dalén, L, 2010. Refugia revisited: individualistic responses of species in space and time. Proc. Roy. Soc. Lond. 277, 661–671.

Thornthwaite, C W, 1948. An approach toward a rational classification of climate. Geogr. Rev. 38, 55–94.

Wäreborn, I, 1969. Land molluscs and their environments in an oligotrophic area in southern Sweden. Oikos 20, 461–479.

Wäreborn, I, 1970. Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. Oikos 21, 285–291.