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The Holocene

Holocene palaeoenvironments from the Direndall tufa (Luxembourg) reconstructed from the molluscan succession and stable isotope records

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Abstract

This paper reports the results of new malacological analyses from a thick tufa sequence at Direndall (Luxembourg). The study is temporally contextualised with radiocarbon dates and an age–depth model. The malacological study focuses on species associations to reconstruct palaeoenvironmental developments. The gradual appearance of several shade-demanding species reflects the expansion of forest environments during the early Holocene. After c. 7.5 cal. kyr BP, three phases of maximal expansion of shade-demanding species are interspersed with two phases of decline of these taxa dated between c. 7.1 and 6.5 cal. kyr BP and between c. 3.5 and 2.4 cal. kyr BP. Malacological data are discussed with previously published calcite stable isotope data from the same sequence. Strong correlations between malacological data and $\delta^{13}C$ profile are highlighted over the whole sequence. Combined influences of local environmental conditions and regional climatic trends are emphasised. The sequence provides a palaeoenvironmental succession free of any anthropic influence.

Keywords

Holocene, Luxembourg, molluscs, palaeoenvironment, stable isotopes, tufa

Introduction

In global climate records of Greenland ice sheets, the Holocene is considered as a rather climate-stable phase (GRIP, NGRIP, GISP2). However, this apparent stability is tempered by the occurrence of cold events detected by ice-drift flux peaks in the North Atlantic (Bond et al., 1997). The transposition of these climate events recorded in glacial and marine contexts to the European continent is deductive. Research conducted on nearly 30 lakes in the Jura mountains, the northern French Alps and the Swiss plateau has highlighted the succession of 15 phases of lake-level

transgression, marking periods of climate deterioration (Magny, 2004). High temporal resolution records of Holocene climate fluctuations have been collected in lacustrine varve formations (e.g. Feeser et al., 2016; Lücke et al., 2003) and speleothems (e.g. McDermott et al., 2001; Mischel et al., 2017). In open-air conditions, tufas are one of the most suitable sedimentary archives to trace the evolution of climate conditions. These freshwater carbonate deposits provide valuable sediment sequences from which stable isotopes record changes in temperatures and humidity (Andrews, 2006). Shells of molluscs are often well-preserved in tufas whereas other biomarkers, such as pollen and seeds, are usually lacking (Dabkowski, 2014). The snail communities lived and died more-or-less where they were found and were weakly affected by transport or diagenetic processes. Various studies demonstrated the increasing contribution of malacological data from tufa to the reconstruction of Holocene palaeoenvironmental developments in Europe (e.g. Alexandrowicz et al., 2016; Gedda, 2001; Kerney et al., 1980; Limondin-Lozouet and Preece, 2004; Meyrick and Preece, 2001; Preece, 1998). Discussion between geochemical and malacological data provided an insight into local environmental changes directly correlated with climate variability (Dabkowski et al., 2019; Garnett et al., 2004; Žák et al., 2002), as tufas are often found in small valleys that were little affected by past human activities. During the second part of the Holocene, a reduction of European tufa deposits, both in deposition rate and occurrence, was suggested and referred as 'the Late-Holocene tufa decline' (Goudie et al., 1993). At Direndall, in Luxembourg, a thick tufa sequence spanned almost the entire Holocene. Meyrick (2000, 2001) analysed the molluscan succession, which showed a broad outline of the sequence, but his counts were extremely low and much of the finer biostratigraphical detail was lost. Consequently, new molluscan analyses have been undertaken through the sequence in order to improve the record from this important site. These new malacological analyses were undertaken in parallel with a study of the stable isotopes from the same profile (Dabkowski et al., 2015), allowing the two datasets to be critically compared and put in perspective with regional vegetation change and climate trends.

Material and method

The Direndall tufa sequence is located at Lorentzweiler (Luxembourg), on the eastern valley slope of the Mamer River, flowing in a steep-side valley, ~ 100 m deep and ~ 300 m large (Figure 1). This valley was incised in the Luxembourg plateau comprised by Early Jurassic deposits. Our studies focused on the western side of a protruding crescent-shape mound of tufa ~ 95 m long and ~ 25 m wide (Dabkowski et al., 2015).

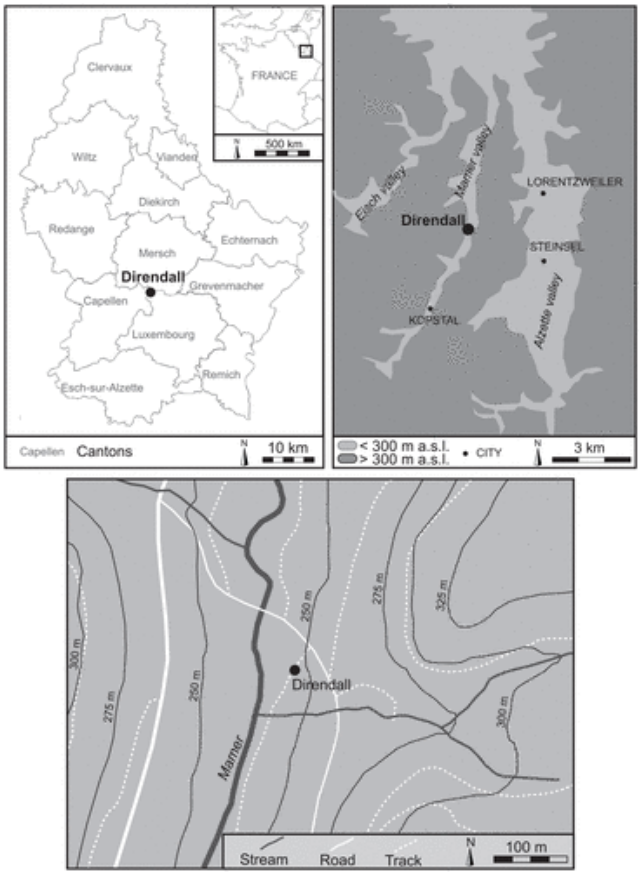

Figure 1. Location maps of Direndall in Luxembourg (top left), in the Mamer valley (top right) and in the local topography (bottom).

Stratigraphy and sampling strategy

The upper 3.7 m of the deposits were observed on an open stratigraphic section at the same place as that investigated by Meyrick (2000). The lower 7 m were drilled by coring ~6 m northward (Figure 2). First, a T6 corer was used but the injection of water into the corer caused the sediment liquefaction. A percussion corer with plastic sheathes was then used. Since the plastic sheathes were shorter than the corer, gaps of 22 cm were observed between cores (Figure 2). The use of the T6 corer for the deepest core, which was driven by technical reasons, resulted in the loss of sediment but allowed the geological bedrock, the Keuper marls (Triassic Period), to be reached.

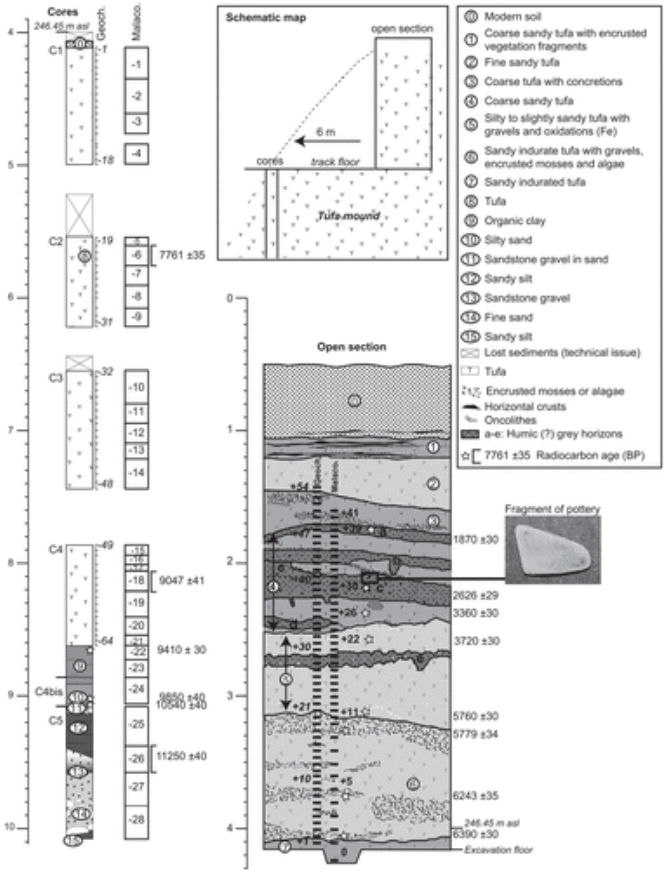

Figure 2. Schematic map of the location of the samples in the tufa mound, stratigraphy with the position of malacological and geochemical samples, radiocarbon dating and photograph of the pottery fragment found in unit 4.

The comprehensive description of the stratigraphy can be found in Dabkowski et al. (2015). The whole succession of tufa facies is typical of a perched springline deposit (Pedley, 1990). Three main sedimentation phases were observed in the cores (Figure 2): (1) sands and sandy silts mixed with sandstone gravels interpreted as fluvial deposits mixed with colluvial inputs (units 15–10), (2) organic-rich clay interpreted as formed in hydromorphic conditions (unit 9) and (3) friable sandy tufa (unit 8). In the upper open section, seven units of tufa were described (Figure 2). The indurated Unit 6, with encrusted mosses and algae, was considered as characteristic of a traverse tufa barrier in a barrage system as described by Casanova (1981) and Pedley (1990). The overlying Unit 5, with fine and friable sediment, was regarded as typical of deposits developed upstream of such barrier (Pedley et al., 1996). The interstratified dark grey layer (e) observed within this unit suggested the development of a humic horizon. Unit 4 was then characterised by a succession of light brownish tufa with oncolites, interpreted as formed in wandering channels, and dark grey tufa with evidence of bioturbations attesting to the development of paleosols. The deposition of indurated tufa with encrusted mosses and algae in Unit 3 suggested the new development of a small barrage. The fine and friable tufa from Unit 2 might be deposited in the upstream of such a dam (as observed in Unit 5). The upper tufa (Unit 1), with encrusted vegetation fragments developed in thin horizontal layers, was considered as formed under paludal conditions (Pedley, 2009; Pedley et al., 2003). Twenty-eight malacological samples ranging in thickness from 5 to 30 cm were extracted from the cores (Figure 2). The weight of samples before sieving was

between 0.4 and 2.9 kg. These thickness variations were guided by sedimentary boundaries, clear in sands and clay, but less easy to discern in the tufa (Figure 2). In the upper profile, 42 malacological samples were extracted every 10 cm between samples 0 and + 9 and every 5 cm between +11 and +41 (Figure 2). The weight of raw sediment before sieving was comprised between 4.2 and 7.9 kg for a standard volume of 5 L of sampled sediment.

Radiocarbon dating and age–depth model

Four radiocarbon dates on charcoal were reported by Meyrick (2000), two in the part of the sequence corresponding to that investigated by drilling in 2013 and two at the top of the upper profile (Dabkowski et al., 2015). The exact correlation between our cores and the profile studied by Meyrick was unclear since they were not made exactly at the same place. The two dates from the upper profile came from levels heavily intruded by roots, raising concerns about contamination. As a result, we have chosen to make a significant effort in providing new dating on our succession.

Fifteen new AMS radiocarbon dates were obtained (Table 1). In the deepest cores, with sand and clay, radiocarbon dates were measured on charcoal, wood and organic sediments (Table 1). In the tufa, charcoal was virtually absent. One date on charcoal in the malacological sample –9 gave an age far too young (Table 1). The other dates were measured on minute shells of gastropods as recommended by Pigati et al. (2010). Each date was measured on about 15 shells of the same species. The shells were broken to facilitate the removal of the tufa filling the shells and ultrasonically cleaned. No inversion was observed along the sequence even though some dates were obtained on different species (Table 1) at an interval of smaller than 20 cm in stratigraphy (Figure 2). The only archaeological evidence recovered within the sequence was a piece of pottery with a paste characteristic of *Terra Belgica* (Reinert, 1992) that was found at the level of the malacological sample +31 (Figure 2). The date of 2626 ± 29 BP obtained from shells in the malacological sample +30 (Table 1) was about a thousand years too old compared with this pottery fragment. However, this small piece of pottery was found under a bed of oncolite and could have been moved by rough water, as suggested by the damaged surface and blunt edges of the ceramic (Figure 2).

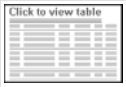

Table 1. Radiocarbon dating. Calibrations were performed with IntCal13 curve (Reimer et al., 2013) in OxCal 4.3.2 (Bronk Ramsey, 2017).

The dates were calibrated using the IntCal13 calibration curve (Reimer et al., 2013) in OxCal 4.3.2 (Bronk Ramsey, 2017). An age–depth model was built using the median values of calibrated 2 σ range BP (Figure 3). In the intervals between dated samples, ages were calculated using the model with a resolution between 1 and 0.5 cm. The command ‘Boundary’ was applied to incorporate sediment transitions into the model. An agreement value of 97% between measured and modelled values was

reached. The model stopped at the level of the malacological sample + 39 since we had no radiocarbon dating for the upper samples.

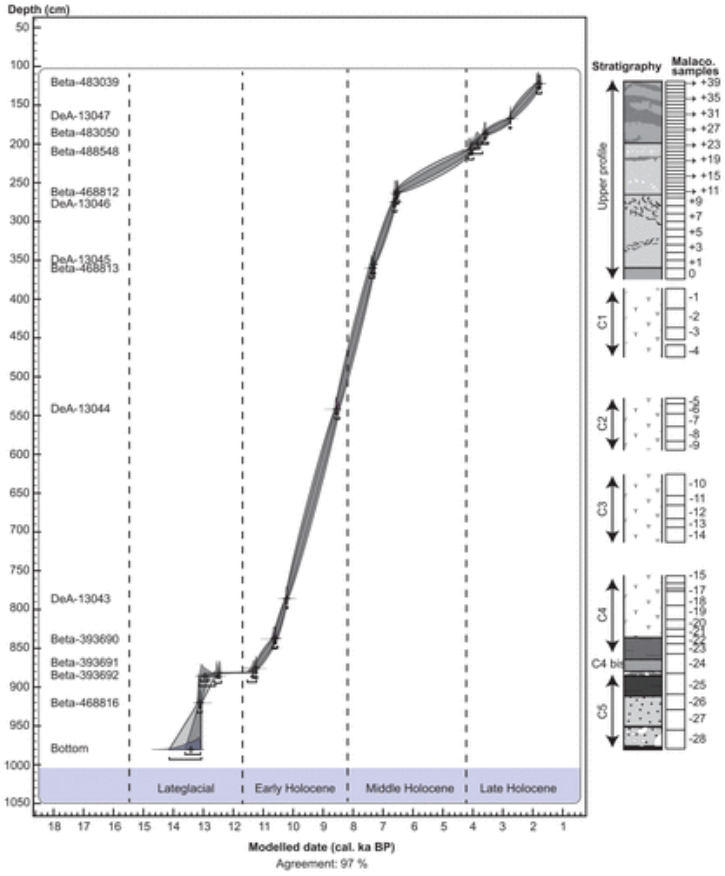

Figure 3. Age–depth model and schematic stratigraphic log of Direndall. For sedimentary description see Figure 2; for dating, see Table 1.

Malacological data

All the samples from cores were fully sorted, except –16, which was lost, and –19, for which only a half has been sorted (Table 2). Samples –28 to −23 were completely free of any shell. In the upper profile, 36 of the 42 samples collected were sorted (Table 3). Between samples +10 and +41, each taken over a thickness of 5 cm, only one sample out of two was first sorted. The resolution was tightened according to variations in the malacological assemblages. Samples that have not been sorted are in portions of the sequence where the assemblages were not subject to significant changes both in their species and ecological composition. For some samples, the volume and weight of sediment to be sorted were so large that an exhaustive sorting was not carried out, as the number of shells collected from one-half or one-quarter of the sample was sufficient to ensure the statistical representativeness of the studied portion. According to the method described by Evans (1972), the sieve sediments with a grain size component between 0.5 and 2 mm were placed flat, ensuring a good mixture of the different fractions and then divided into eight portions, at least two of which were studied.

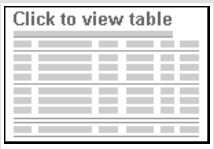

Table 2. List of fauna and modelled ages of samples from the coring section.

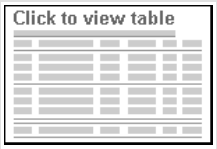

Table 3. List of fauna and modelled ages of samples from the upper profile.

Land snails were represented by at least 55 taxa and freshwater molluscs by only 3 (Tables 1 and 2). Determination and ecological requirements of species were based on literature (Horsák et al., 2013; Welter-Schultes, 2012; Wiese, 2014). The genera *Cepaea, Arianta* and *Bradybaena* were mixed because it was often difficult to differentiate these taxa based on broken shells. For *Nesovitrea*, the presence of *Nesovitrea hammonis* and *Nesovitrea petronella* was suspected in some samples. To mark this uncertainty, the mention 'agg.' was added to *Nesovitrea hammonis*, the most common species of the genus *Nesovitrea* at Direndall. The mention 'agg.' was also added to the species *Euconulus fulvus*, which could have been mixed with *Euconulus alderi* in some samples. Other genera were followed by the mention 'sp.' because the recovered shells were too fragmented for species determination. For *Clausilia* and *Macrogastra*, fragmentation and encrustation of shells had often precluded species determination. Limacidae and Milacidae were mixed as 'slugs'.

Most of the samples taken from the cores yielded counts below the threshold of representativeness of a fossil sample set at 150 individuals by Evans (1972). A presence/absence diagram of species allowed the development of biodiversity between samples –22 and –1 to be tracked (Figure 4). All the samples from the upper profile provided enough shells to draw a diagram showing the proportions of each taxon (Figure 5). For the sake of readability of this diagram, some species with comparable environmental requirements have been combined. For the coring section, samples with small numbers of individuals were merged.

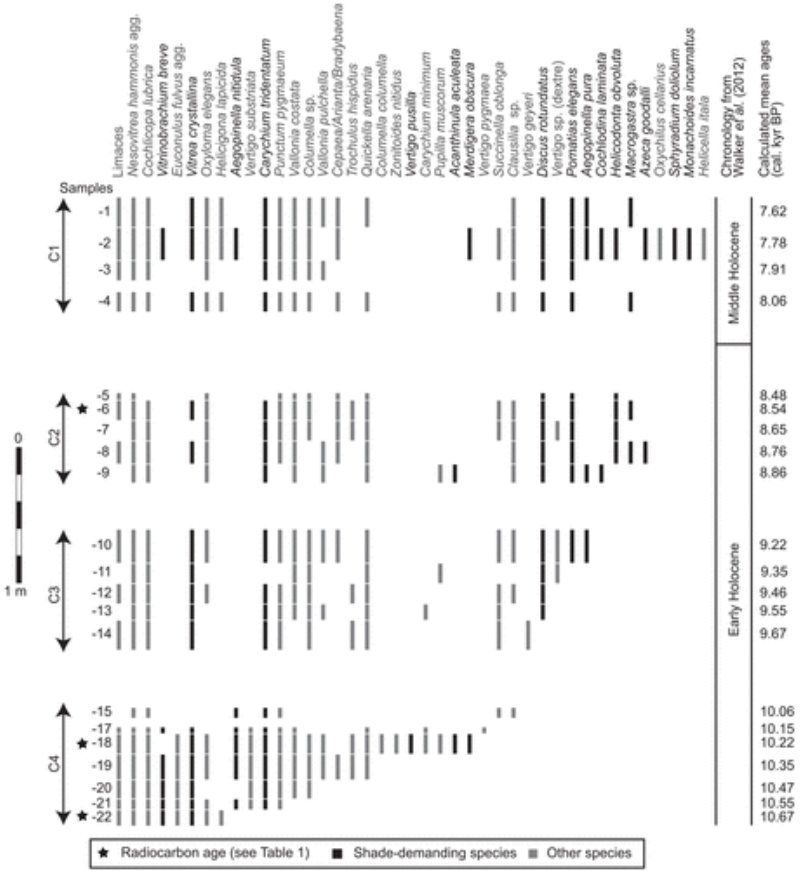

Figure 4. Presence/absence diagram of species recovered in the samples from the coring section.

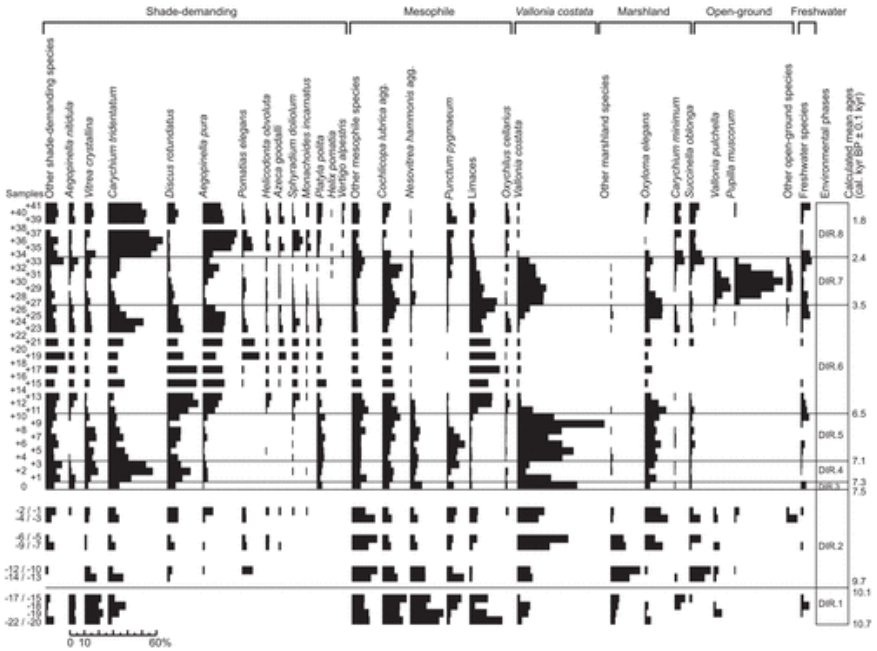

Figure 5. Variations in proportions of some key species and group of species.

Results

Unfavourable conditions for mollusc development and shell preservation

The samples 28 to 24, from cores C5 and C4bis, are sterile. These samples were extracted from sandy sedimentary units (Figure 2). The absence of shells suggests unfavourable conditions for the development of molluscs or the preservation of

shells. The radiocarbon dates allow these samples to be assigned to the late glacial and the beginning of the early Holocene (Table 1). The two periods are separated by a sedimentary hiatus spanning about 1000 years (Figure 3).

Phase DIR.1, between 10.7 and 10.1/9.7 cal. kyr BP: Mesophile species and first shade-demanding species

In the organic-rich clay from the base of the core C4, the sample -23 is sterile. The first sample with shells (–22) comes from the upper part of this clayey unit (Figure 2). The faunal list, composed of 45 specimens divided into 8 taxa, is dominated by slugs (Table 2). These molluscs without external shell are found with species characterised by thin shells (*Nesovitrea hammonis* agg., *Vitrea crystallina, Vitrinobrachium breve*). This assemblage is the initial phase of the malacological succession at Direndall and indicates the onset of plant colonisation. In samples –22 to −17, mesophile taxa are predominant (Figure 4). Within the group of the shade-demanding species, *Aegopinella nitidula* and *Carychium tridentatum* appeared in c. 10.5 cal. kyr BP (sample –21) and *Acanthinula aculeata, Merdigera obscura* and *Vertigo pusilla* c. 10.2 cal. kyr BP (sample –18). Such an increase in the biodiversity of shade-demanding species is a sign of an expansion of forest habitats.

Phase DIR.2, between 10.1/9.7 and 7.5 cal. kyr BP: Marshland species and new shade-demanding species

The base of the environmental phase DIR.2 is defined by the expansion of marshland species (mainly from the Succineidae family) in –14, which is a persistent feature until –1 (Table 2). Thirteen new taxa are recovered within this phase and most of them are forest species (Figure 4). Within this ecological group, *Discus rotundatus* appeared in c. 9.5 cal. kyr BP, *Pomatias elegans* and *Aegopinella pura* c. 9.2 cal. kyr BP, *Cochlodina laminata* c. 8.9 cal. kyr BP, *Helicodonta obvoluta, Macrogastra* sp. and *Azeca goodalli* c. 8.8 cal. kyr BP, and *Sphyradium doliolum* and *Monachoides incarnatus* c. 7.8 cal. kyr BP. The timing of these appearances should be considered with caution, as the samples provide assemblages with low abundances (Table 2). Such an increase in biodiversity indicates the development of a forest with deep shade.

Phase DIR.3, between 7.5 and 7.3 cal. kyr BP: Expansion of *Vallonia costata* and appearance of *Platyla polita*

This environmental phase is based on the composition of the malacological fauna recovered in sample 0. A sharp increase in *Vallonia costata* proportions is observed together with a sharp decrease in proportions of marshland species (Figure 5). All the open-ground species and some of the forest species found in the preceding phase are lacking. This simultaneous decline in biodiversity in these two groups of species can be explained by drier conditions. *Platyla polita*, inhabiting today moderately humid forests, occurs during this phase.

DIR.4, between 7.3 and 7.1 cal. kyr BP: Shade-demanding species with

Carychium tridentatum and Discus rotundatus as main species

Samples +1 to +3 are characterised by increasing proportions of shade-demanding species that develop at the expense of *Vallonia costata* (Figure 5). *Carychium tridentatum* shows the highest proportions. Its association with *Discus rotundatus* and *Vitrea crystallina* suggests the development of a moist forest litter that could be related to the expansion of a deciduous forest. The appearance of *Ena montana* in sample +2 (Table 2) is consistent with this assumption since this species mainly inhabits today broadleaf forests.

DIR.5, between 7.1 and 6.5 cal. kyr BP: Decrease in *Carychium tridentatum*, increase in *Vallonia costata*

In samples +4 to +11, the proportions of *Carychium tridentatum* decline while those of *Vallonia costata* increase (Figure 5). The decline of the hygrophilous *C. tridentatum* and the expansion of *V. costata*, living in drier conditions, might suggest a moisture reduction of the floor litter.

DIR.6, between 6.5 and 3.5 cal. kyr BP: Shade-demanding species with *Discus rotundatus* and *Aegopinella pura* as main species

The proportions and diversity of forest species increase significantly in samples +11 to +26 (Figure 5). In this ecological group, *Discus rotundatus* and *Aegopinella pura* are the main taxa. *Aegopinella pura* is found today in moist forest. Such a palaeoenvironmental reconstruction hypothesis would be consistent with the increase in the proportions of slugs that, devoid of an external shell, have high moisture requirements. In samples +25 and +26, the decrease in proportions of shade-demanding species marks the transitional phase between DIR.6 and DIR.7.

DIR.7, between 3.5 and 2.4 cal. kyr BP: Expansion of *Vallonia costata* and *Pupilla muscorum*

This phase is characterised by a decrease in the proportions of shade-demanding species, mainly in favour of *Vallonia costata* and the open-ground species *Pupilla muscorum* (Figure 5). These malacological developments reflect a phase of forest clearing. In samples +31 and +32, the proportions of open-ground species decrease while those of shade-demanding species increase. These two samples initiate a new phase of forest expansion.

DIR.8, after 2.4 cal. kyr BP: Shade-demanding species with *Carychium tridentatum* and *Aegopinella pura* as main species

A new development of shade-demanding species is observed in samples +34 to +41 (Figure 5). *Carychium tridentatum* and *Aegopinella pura* are the main species. These two species live today in moist habitats. *Vallonia costata*, which prefers drier locations, and the open-ground species are virtually absent.

Discussion

Discussion with local stable isotope records

The new malacological data recovered at Direndall provide detailed environmental information that can be discussed with much higher confidence to climatic records than the Meyrick's malacological data originally used in Dabkowski et al. (2015). As observed in Dabkowski et al. (2015), *correlations between the $\delta^{18}O$ profile and the malacological records are sparse*. The main correlation found is the increase in the number of forest species as a consequence of the early Holocene warming (Figure 6). However, this connection was evident since tree vegetation could not grow until postglacial conditions were established.

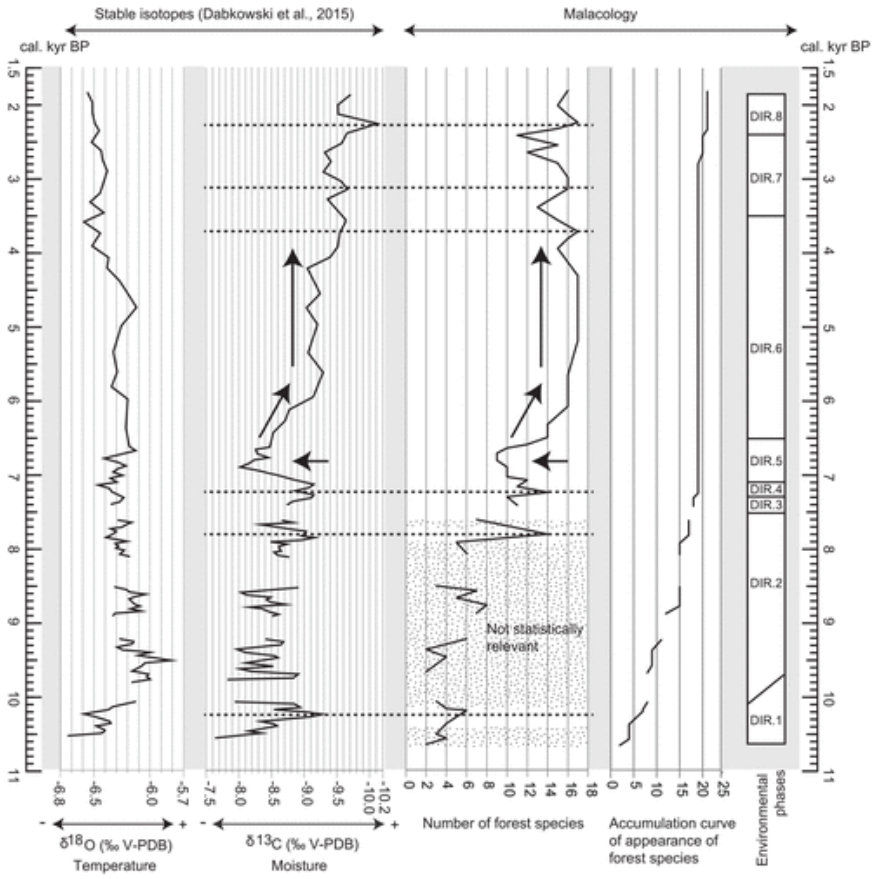

Figure 6. Variations in oxygen and carbon stable isotopes from tufa calcite with regard to variations of forest species biodiversity and main environmental phases.

The dashed lines illustrate areas of convergence between the $\delta^{13}C$ profile and changes in the number of forest species. The accumulation curve of forest species tracks the timing of the appearance of these species within the sequence.

There is much more to be said about the connection between molluscan record and $\delta^{13}C$ profile. A strong correlation is observed between the number of shade-demanding species and the $\delta^{13}C$ profile. Increased diversity of forest species is observed during periods of increased humidity. In the coring section, the abundance of shells is too low to accurately discuss changes in fauna and in $\delta^{13}C$ profile, except for samples –19, –18 and –2. Increased humidity and biodiversity are observed in samples –18 and –2, respectively, dating from 10.2 and 7.8 cal. kyr BP. One might

think that this increase in biodiversity would be caused by the higher counts in these samples. However, the recurrence of this biodiversity/humidity relationship throughout the sequence suggests that the observations made in the core section are valid. In the upper profile, in addition to providing assemblages with more shells, the malacological samples were also taken in the same (or almost the same) sampling interval as the geochemical samples (Figure 2). Between 7.1 and 6.5 cal. kyr BP (zone DIR.5), a decline of the number of shade-demanding species is coincident with a reduction of moisture (Figure 6). Between 6.5 and 3.5 kyr cal. BP (zone DIR.6), there is first an increase in biodiversity and humidity, and then both are stabilised. During the late-Holocene, the number of shade-demanding species became more uneven, while humidity increased but the three most biodiverse periods correspond to moisture peaks (3.7, 3.1 and 2.3 cal. kyr BP).

Development of forest between 10.7 and 7.5 cal. kyr BP

At Direndall, the absence of botanical remains in the tufa prevented a direct insight into the precise composition of the vegetation cover. However, a discussion of local malacological and geochemical results with regional palaeobotanical data is of relevance. At Waldbillig, 20 km northeast of Direndall, open woodland dominated by *Pinus sylvestris* was reconstructed from a charcoal sequence dating from the first part of the early Holocene (Pernaud, 2001). At Direndall, the occurrence of *Vertigo substriata* in samples –21 to −17 might suggest a plant cover dominated by *Pinus*. In Poland, *Vertigo substriata* was a frequent component of the molluscan assemblages from the early Holocene boreal forest (Alexandrowicz, 2009). At Direndall, this species completely disappeared shortly after 10.2 cal. kyr BP (Figure 4), and its disappearance may be indicative of changes in the composition of the vegetation cover. Between 10.2 and 7.5 cal. kyr BP, a gradual increase in shade-demanding species diversity is observed. This development is coincident with the establishment of deciduous forests reconstructed in regional pollen records through the decline of *Pinus* and the expansion of *Corylus* after 10.2 cal. kyr BP (Slotboom and Van Mourik, 2015).

The progressive development of forest environments was extensively observed in numerous malacological successions over Central and Western Europe (Alexandrowicz, 2009; Horáček and Ložek, 1988; Limondin-Lozouet and Preece, 2004; Preece, 1998). In these two large areas, there was a pool of species in common, but several shade-demanding species showed a smaller geographical distribution. At Direndall, we recovered some species with a western distribution, such as *Azeca goodalli* and *Pomatias elegans*. These two species were absent from the Holocene successions from the Czech and Slovak Republics (Juřičková et al., 2014a) whereas they were recovered in Northern France (Limondin-Lozouet and Preece, 2004) and in Southern England (Evans, 1972). A reverse pattern was observed for the eastern species *Platyla polita* and *Monachoides incarnatus*. Direndall thus appears as a succession at the crossroads of Atlantic and Continental climate influence. This sequence has recently been integrated into a synthesis of Holocene malacological data comparing the ecological and specific compositions of

European assemblages. Luxembourg and eastern France have emerged as key territories for the assessment of colonisation pathways of shade-demanding species during the Holocene across temperate Europe (Horsák et al., 2019).

Changing environmental conditions between 7.5 and 3.5 cal. kyr BP

During the phase DIR.4, dated between c. 7.4 and 7.1 cal. kyr BP, the association of *Carychium tridentatum* and *Discus rotundatus* suggested the development of a moist forest litter. During the next phase (DIR.5), the decline of the hygrophilous species *Carychium tridentatum* and the expansion of *Vallonia costata*, preferring drier conditions, suggested a period of relative reduction of the soil moisture. This assertion was strengthened by the reduction of moisture expressed in the $\delta^{13}C$ profile. The reconstruction of drier conditions between c. 7.1 and 6.5 cal. kyr BP is consistent with the estimate of a significant decrease in both winter and summer precipitation derived from pollen data at Echternach, 25 km northwest of Direndall (Guiot and Couteaux, 1992). At Waldbillig, 20 km northeast of Direndall, a recent review of pollen data collected by Heim in 1992 (Gaudin, 2018) found 90% of arboreal pollen with a strong dominance of *Corylus*, which is characteristic of light woodland areas and tolerant to drought. Such a prevalence of *Corylus* had already been observed in the pollen data from Berdof (Schwenninger, 1989) and Echternach (Couteaux, 1970) dating from the same period. This dry excursion observed in Luxembourg is contemporaneous with a long low lake-level phase in the Jura, northern French pre-Alps and Swiss Plateau (Magny, 2004). After c. 6.5 cal. kyr BP (phase DIR.6), the development of *Aegopinella pura* refers to moister forest habitats. Up to 6.0 cal. kyr BP, the proportions of shade-demanding species increase in strict correspondence with moisture conditions reconstructed from the $\delta^{13}C$ profile. This shift in moisture conditions is coincident with the local development of the *Quercetum mixtum* inferred from the pollen data from the Gutland region (Slotboom and Van Mourik, 2015). After 6.0 cal. kyr BP, which is the end of the middle-Holocene thermal optimum in Central-Western Europe (Davis et al., 2003), malacological data and $\delta^{13}C$ profile are broadly stabilised up to c. 4.0 cal. kyr BP. This date broadly corresponds with a shift towards colder conditions in the $\delta^{18}O$ profile. In Luxembourg, *Fagus* expansion is observed during the same period in regional pollen data (Couteaux, 1970; Slotboom and Van Mourik, 2015). In southern Germany and lowland Switzerland, pulses in the expansion of *Fagus* were precisely observed during cold and wet episodes of the first part of the late-Holocene (Tinner and Lotter, 2006).

A place under a low anthropogenic influence during the late-Holocene?

In Meyrick (2000), the mollusc zone Dir4, which spanned both the middle and the late-Holocene, was divided into three subzones: Dir4a and Dir4c, marking forest optimum phases, were interspersed with an episode of forest clearance (Dir4b). In our new study, three phases of forest expansion interspersed with two phases of forest clearing were reconstructed. The higher counts recovered in our new samples made this more accurate zonation scheme possible. The clearing episode suggested

by Meyrick (2000), corresponding to the phase DIR.7, is better defined from a malacological and chronological perspective. This phase was originally assumed to be of Roman origin (Meyrick, 2000). In our new study, this phase is dated between 3.5 and 2.4 cal. kyr BP, that is, between the middle of the Bronze Age and the middle of the Iron Age. One could hypothesise an anthropogenic phase of forest clearance, especially since a human-induced expansion of grasslands was widely observed in north-western Europe during this period (Granai and Limondin-Lozouet, 2018). However, there is no evidence of human settlement in the vicinity of the sequence or of landscape opening at the same time in Waldbillig's charcoal data (Pernaud, 2001) and Echternach's pollen data (Couteaux, 1970), both located around 20 km away. At Direndall, the phase of landscape openness seems to be rather related to local geomorphological parameters. The phase DIR.7 was reconstructed within the sedimentary unit 4, which was characterised by alternating dark grey tufa levels and light brownish tufa levels with oncolites deposited in wandering channels. It can be hypothesised that the phase of forest clearance inferred from the molluscan assemblages was the result of a local phenomenon, which was related to the exposure of the soil by erosion in the vicinity of the channels. The new development of shade-demanding species during the phase DIR.8 reflects the small spatial coverage of the vegetation openness. All forest species present in the previous phases return to the sampling location, indicating the unaltered nature of the surrounding forest cover. Shade-demanding species diversity remains broadly unchanged until at least 1.8 cal. kyr BP. The site is still located today in a forest environment. The Direndall molluscan succession has thus shed light on the late-Holocene palaeoenvironmental developments observed in contexts under low anthropogenic influence.

Conclusion

The molluscan succession of Direndall is the longest and best-dated Holocene succession at a regional scale. This reference series can be used as a basis for comparison with the molluscan successions studied further west (the United Kingdom and France) and further east (Poland, Czech and Slovak Republics). Species with a western European distribution and species with an eastern European distribution were found. This peculiarity highlighted the key position of the Luxembourg and neighbouring regions for tracking the colonisation pathways of forest species during the Holocene across temperate Europe. Regarding the second part of the Holocene, forest environments were mainly observed so far in mountainous regions under a low anthropogenic influence such as in the Carpathians (Alexandrowicz et al., 2016; Juřičková et al., 2018) and the Sudetes (Juřičková et al., 2014b). Conversely, open environments were reconstructed in places under stronger human influence, particularly in floodplains (e.g. Alexandrowicz, 2013; Granai and Limondin-Lozouet, 2014; Juřičková et al., 2013). At Direndall, forest environments persisted during the second part of the Holocene. However, almost no new forest species colonise the site after the middle-Holocene climate optimum. Most species appear during the Early Holocene warming phase.

The combination of malacological and geochemical investigations highlighted the positive correlation between variations of $\delta^{13}C$ and those of shade-demanding molluscs. Phases of expansion of proportions of forest species were correlated to increasing moisture conditions in the $\delta^{13}C$ profile. Conversely, the first phase of regression of these taxa was correlated to decreasing moisture conditions between 7.1 and 6.5 cal. kyr BP. The second phase of decline of shade-demanding taxa, between 3.5 and 2.4 cal. kyr BP, was interpreted as resulting from a local exposure of the soil in connection with a wandering channel. Influences of local environmental conditions and regional climatic trends were thus emphasised. Changes in vegetation composition were hypothesised based on variations in malacological assemblages and then discussed with Holocene climate dynamics. However, at the regional scale, we still lack a reference series with both botanical and malacological records.

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