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# Palaeoenvironmental dynamics of the MIS 11 interglacial in north-western Europe based on the malacological succession from La Celle (Seine Valley, France): Relationship with glacial refugia and palaeobiodiversity

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## Highlights

- The *Lyrodiscus* mollusc fauna is a biochronological reference for MIS 11 in NW Europe
- La Celle is the sole deposit yielding a detailed record of MIS 11 forest expansion
- Atlantic and Central refuges are the main sources of mollusc recolonization in NW Eur
- Strict Mediterranean species reach NW Europe only at the climatic optimum
- The malacological diversity hotspot during MIS 11 extends further north in NW Europe

## Abstract

In north-western Europe, continental records of Pleistocene interglacials are well preserved in fluvial sequences and particularly within calcareous tufas that formed at the top of the series. They are the sole deposits recording the full optima. Tufas contain rich malacological communities that allow the detailed palaeoenvironmental history of past interglacials to be reconstructed. Several tufas have been investigated in the study area, which have led to the recognition of the « *Lyrodiscus* fauna » as a characteristic biostratigraphical signature of tufa sequences of MIS 11 age in north-western Europe. Among these, the site at La Celle in the Seine valley (France) is the only one where tufa has accumulated a substantial thickness (almost 9 m) in which the complete development of the *Lyrodiscus* fauna is represented, yielding a detailed record of the forest expansion during the MIS 11 interglacial. The La Celle succession therefore provides a regional framework into which other sequences can be set, shedding lights on various aspects of palaeoenvironmental dynamics, biostratigraphy, palaeogeography and palaeobiodiversity. Combined malacological and isotopic records from La Celle demonstrate a close correlation between increasing temperatures and the development of forest land snail communities.

The palaeoecological framework of forest extension inferred from the malacological succession of La Celle allows the shorter successions from northern France and south-eastern England to be located within the maximum development of the humid forest biotope during MIS 11c. The order of occurrence of forest snails indicates that Atlantic and Central European refugia are the original sources of recolonizations for north-western European sites. Strict Mediterranean species reach the area only at the MIS 11c climatic optimum. Many species present during MIS 11c no longer live in this part of Europe, indicating a northward shift in the location of the modern alpine biodiversity hotspot.

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## Keywords

Land snails; Biostratigraphy; Middle Pleistocene; Palaeogeography; Calcareous tufa; *Lyrodiscus*

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### 1. Introduction

From the Mid-Pleistocene Transition and the shift to 100 kyr climatic cycles, the impact of glacial advances on the plant and animal communities of north-western Europe is greatly amplified (e.g. [Head and Gibbard, 2005](#)). During glacial periods, this area occupies a particular geographical position near the front of the ice-sheets that lead to its transformation into a polar desert ([Toucanne et al., 2009](#)), in which aeolian dust is drifted during stormy events leading to thick loess deposition ([Antoine et al., 2009](#)). In turn, this situation causes modifications in the geographical distribution of organisms and many taxa retreat to southern glacial refugia (e.g. [Bennett et al., 1991](#); [Tzedakis et al., 2013](#)) while others survive in northern micro-zones ([Schmitt and Varga, 2012](#)).

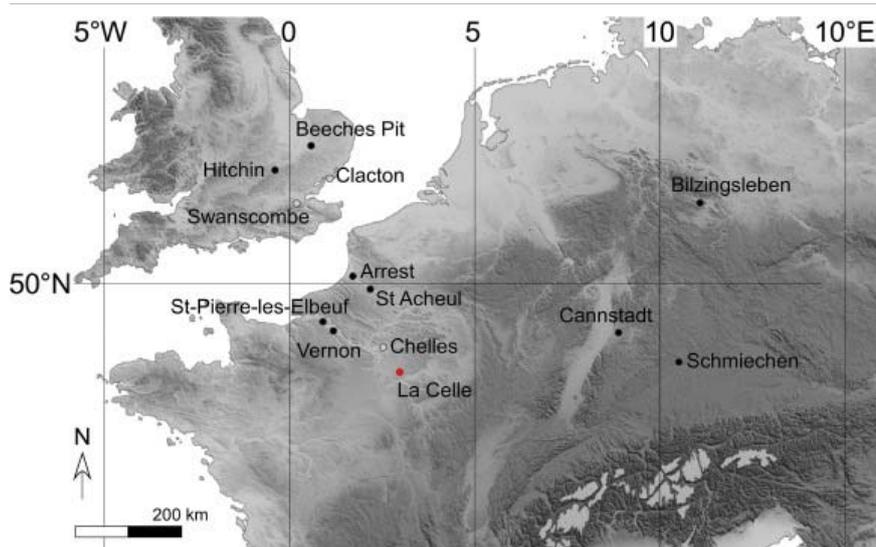
Conversely, each interglacial period is characterized by the recolonization of the territory by living organisms with the expansion of forest biotopes. However many studies have demonstrated that interglacial periods differ in duration, intensity, seasonality and internal variability, but a general theory accounting for this diversity remains elusive ([Tzedakis et al., 2009](#)). Noticeable differences in biodiversity and associated palaeoenvironmental conditions therefore occur during Middle Pleistocene interglacials.

Reconstructing interglacial palaeoenvironmental dynamics in north-western Europe is complicated by the absence of long lacustrine or peat sequences that could provide continuous pollen records such as occur in southern regions (e.g. [Beaulieu et al., 2001](#); [Desprat, 2007](#)). In this northern area, long continental sequences derived mainly from loess accumulation (e.g. [Lautridou et al., 1974](#); [Antoine et al., 2003a](#), [Antoine et al., 2003b](#)). However, in such aeolian sediments interglacials are generally represented by fully decalcified paleosols in which fossil remains are never preserved. Temperate periods are better represented in fluvial sequences in which tufa formations can provide long and detailed records of Pleistocene interglacials and are the only deposits that cover climatic optima ([Antoine and Limondin-Lozouet, 2004](#)). Although usually lacking pollen, these calcareous deposits contain a diverse range of fossils and are particularly favourable for the preservation of rich molluscan communities ([Preece, 1991](#); [Dabkowski, 2014](#)). Continental molluscs are identifiable to species level and enable detailed palaeoenvironmental reconstructions, as well as evaluations of differences in biodiversity and palaeogeographical history between interglacials (e.g. [Mania, 1995b](#); [Preece et al., 2007](#); [Limondin-Lozouet and Preece, 2014](#)). Land snails are strictly dependent on vegetation and their assemblages are therefore representative of the structure of the vegetation cover. Their palaeoenvironmental interpretation is thus easily comparable to those derived from vegetation proxies in neighbouring regions. Since interglacial malacological successions essentially follow the development of forest, they show common patterns but there are differences between interglacials with respect to the presence of extinct taxa and the order of appearance of particular species. Additionally the geographical distribution of some thermophilous snails may differ between interglacials. These various elements help to identify malacological assemblages characteristic of each interglacial period ([Puisségur, 1976](#); [Mania, 1995a](#); [Ložek, 2000](#)). The recognition of these “malacological signatures” is, however, highly dependent on the quality of the records from various temperate periods, and especially whether tufa sediments have been analysed ([Limondin-Lozouet and Preece, 2014](#)). During the last thirty years or so, detailed malacological investigations have been undertaken on a number of tufa sequences attributed to MIS 11 that form a transect from Britain to Germany ([Kerney, 1959](#), [Kerney, 1971](#); [Mania et al., 2001](#); [Preece et al., 2007](#); [Rousseau et al., 1992](#); [Limondin-Lozouet and Antoine, 2006](#)). Western sequences are characterized by the so-called “*Lyrodiscus* assemblage” that has been recognized as a reliable age-diagnostic molluscan fauna of the MIS 11 interglacial ([Rousseau et al., 1992](#); [Limondin-Lozouet and Antoine, 2006](#); [Preece et al., 2007](#); [Cliquet et al., 2009](#); [Limondin-Lozouet, 2017](#)). Of these western tufas, the La Celle sequence is the best developed with a cumulative thickness of almost nine metres, when other sequences

rarely exceed 1–2 m in height. It therefore provides a unique opportunity to document how the *Lyrodiscus* fauna appeared and developed allowing an assessment of the biodiversity of the group, and to reconstruct in detail the palaeoenvironment evolution in north-western European valleys during MIS 11. This paper presents a detailed account of the malacological succession from La Celle, which reflects the progressive development of the vegetation cover and provides a framework within which records from neighbouring sites can be set. The successive appearance of different groups of thermophilous species is discussed and probable dispersal routes from separate refugia are highlighted.

## 2. Site context, stratigraphy, dating and sampling

The tufa sequence at La Celle (Lat 48°23 N; Long 2°50 E) was deposited from springs emanating from the right bank of the Seine valley about 90 km upstream from Paris (Fig. 1). The lower part of the tufa rests on a middle fluvial terrace of the Seine about 15 m above the modern floodplain, whereas the upper levels of the tufa directly overlie calcareous Eocene bedrock. The tufa covers an area of about 12.5 ha and has a thickness varying between 8 and 15 m (Tournouër, 1877; Bourdier et al., 1969).



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Fig. 1. Location map of La Celle (red dot), other tufa deposits (black dots) and fluvial sequences (grey dots) yielding MIS 11 terrestrial malacofaunas in North-West Europe. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

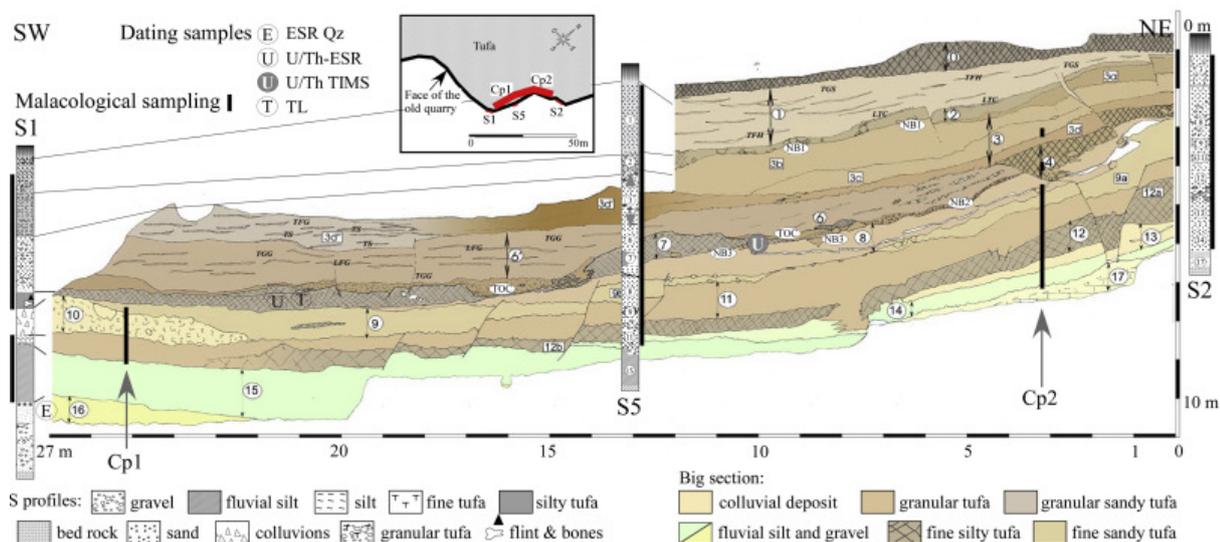
Studies in the 19th and 20th centuries concluded that the tufa formed during a Pleistocene interglacial, but no detailed biostratigraphical study were undertaken and the question of its precise age was left open. In 2003 new multidisciplinary investigations were initiated on the tufa to shed further light on the stratigraphy, palaeontology, geochemistry, and archaeology, and to provide firm conclusions about its age. The development of forest environments reflected by the molluscan succession and occurrence of thermophilous mammals (*Macaca* and *Hippopotamus*) together with a temperate flora including several Mediterranean taxa (fruit and leaf impressions of *Buxus* and *Ficus*), demonstrated full interglacial conditions (Limondin-Lozouet et al., 2006; Jolly-Saad et al., 2006). Geochemical data (stable isotopes and trace elements in tufa calcite) reflect a warm and wet climatic optimum contemporaneous with closed forest environment, followed by two temperature decreases associated with oscillations in humidity (Dabkowski et al., 2012). An Acheulean flint industry was recovered from a unit of grey tufa in the middle of the sequence; the associated palaeontological remains and geochemical data indicated that human occupation occurred during the climatic optimum (Limondin-Lozouet et al., 2010; Limondin-Lozouet et al., 2015; Dabkowski et al., 2012).

The tufa was thought to have accumulated during Marine Isotopic Stage 11, a conclusion based primarily on its position within the Seine terrace system and on its malacological content (Lautridou et al., 1999; Limondin-Lozouet et al., 2006). This attribution has been confirmed by a series of radiometric dates reinforced by luminescence measurements (Bahain et al., 2010; Limondin-Lozouet et al., 2010). Five methods applied to four materials give consistent results indicating an average age of 400 ka for the tufa (Table 1). The stratigraphical succession was initially observed from three limited profiles excavated along the slope, but subsequently a 27 m long section was created that allowed precise correlations of

the sedimentary units and a better reconstruction of the formation dynamics. The recently observed sequence, described in detail in [Limondin-Lozouet et al. \(2010\)](#), represents a total thickness of 9 m ([Fig. 2](#)).

Table 1. Details of dates from La Celle.

Profile	Level	Material	Method	Result
<b>Main section</b>	16: fluvial sand	Sand	ESR Qz	449 ± 60 ka
	7: fine grey tufa	Horse tooth	U/Th-ESR	420 (+46/-44) ka
	7: fine grey tufa	Heated flint	TL	418 ± 48 ka
	NB3: block layer	Indurated tufa	U/Th TIMS	388.4 (+51/-34) ka
<b>S4</b>	Upper part of the tufa	Indurated tufa	U/Th TIMS	387.5 (+88.8/-48.1) ka
	Upper part of the tufa	Indurated tufa	U/Th	> 350 ka



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**Fig. 2.** Stratigraphy of the tufa deposit at La Celle. Previous profiles created in 2003 are plotted against the large section excavated in 2007. Sampling for malacology, indicated by black lines, was undertaken first along the S1, S5, S2 profiles and subsequently completed along the large section (Cp1, Cp2). Geochronological measurements are given on [Table 1](#).

**Lithology:** 0 Top soil. 1, 2 and 3 Granular sandy tufa yellow, light brown, orange. 4, 7 and 12 Fine grey silty tufa. 5 and 6 Granular tufa light brown and light grey-brown. NB1 to NB3 Block levels. 8 and 9 Fine sandy tufa light brown and light orange. 10 Colluvial tufaceous deposit. 11 Granular sandy tufa light brown. 13 and 14 Fine silty tufa light yellow and white. 15 and 16 fluvial silt and gravels. 17 Calcareous bedrock. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Palaeoenvironmental reconstructions inferred from the malacological succession at La Celle were based on the revision of the old collections ([Limondin-Lozouet et al., 2006](#)) and on data obtained from the three new profiles ([Limondin-Lozouet et al., 2010](#), [Limondin-Lozouet et al., 2015](#)). These three profiles, S1, S5, S2, located respectively at the base, the middle part and the top of the slope ([Fig. 2](#)) were sampled continuously at a 10 to 20 cm resolution depending on tufa lithology. Complementary samples were taken in the basal part of profile S1 at a higher resolution of 5 cm to identify the precise appearance of molluscan communities within the basal fluvial silt (unit 15).

Detailed malacological analyses from the 27 m long profile are reported here for the first time. Two new profiles were thus studied continuously at 10 to 20 cm intervals ([Fig. 2](#): Cp1, Cp2), as well as two additional bulk samples in levels 4 and 3, to

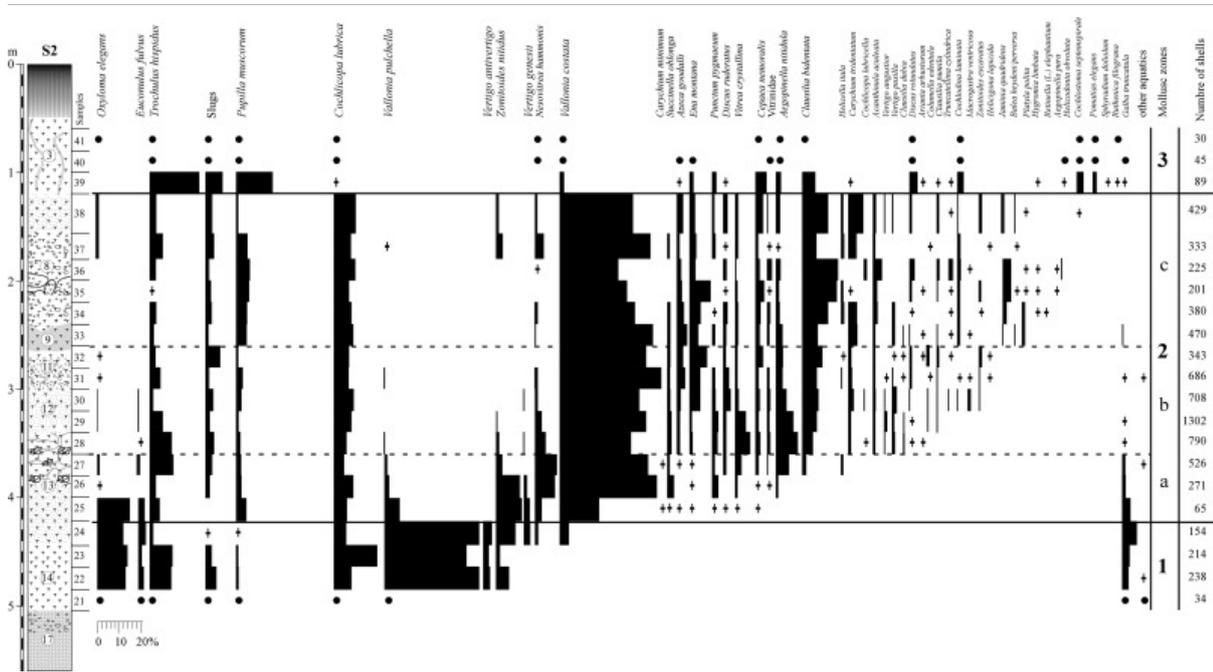
complete the profile Cp 2 (Fig. 2).

Samples of 5 kg weight were analysed for molluscs according to standard procedures: wet sieving on a 0.5 mm mesh and minimum totals based on both complete shells and fragments (Puisségur, 1976). The complete palaeoenvironmental data presented here is based on the study of 120 samples yielding 42,074 individuals belonging to 103 taxa, 94 of which can be assigned to species. Detailed counts are available as supplementary data (Tables S1 to S5).

### 3. Molluscan analyses of the La Celle succession: Results and discussion

#### 3.1. Biostratigraphical approach: The malacological zonation

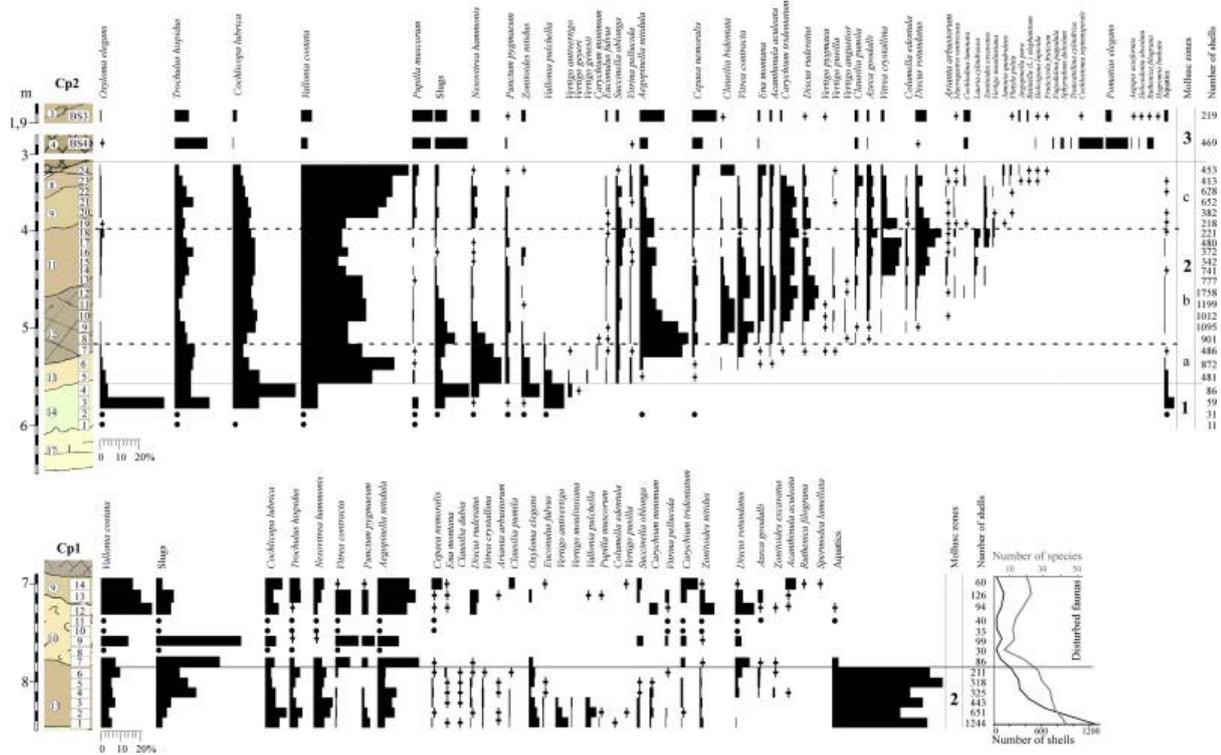
The malacological assemblages were plotted as percentage frequency histograms, except when the total number of shells in a sample failed to reach 50, in this case the presence of a species is indicated by a single dot (Fig. 3, Fig. 4, Fig. 5, Fig. 6). Similar changes can be observed in the composition of assemblages from the different profiles prompting the definition of a biozonation for the site. The molluscan succession can be divided into four biozones based on the occurrence and/or maximum development of particular species and/or on their disappearance throughout the sequence.



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Fig. 3. Mollusc diagram from La Celle profile S2. Frequencies of taxa are expressed in percentages. Crosses represent single shells; dots show the presence of taxa in samples yielding low numbers of shells (<50). See Fig. 2 for lithology.



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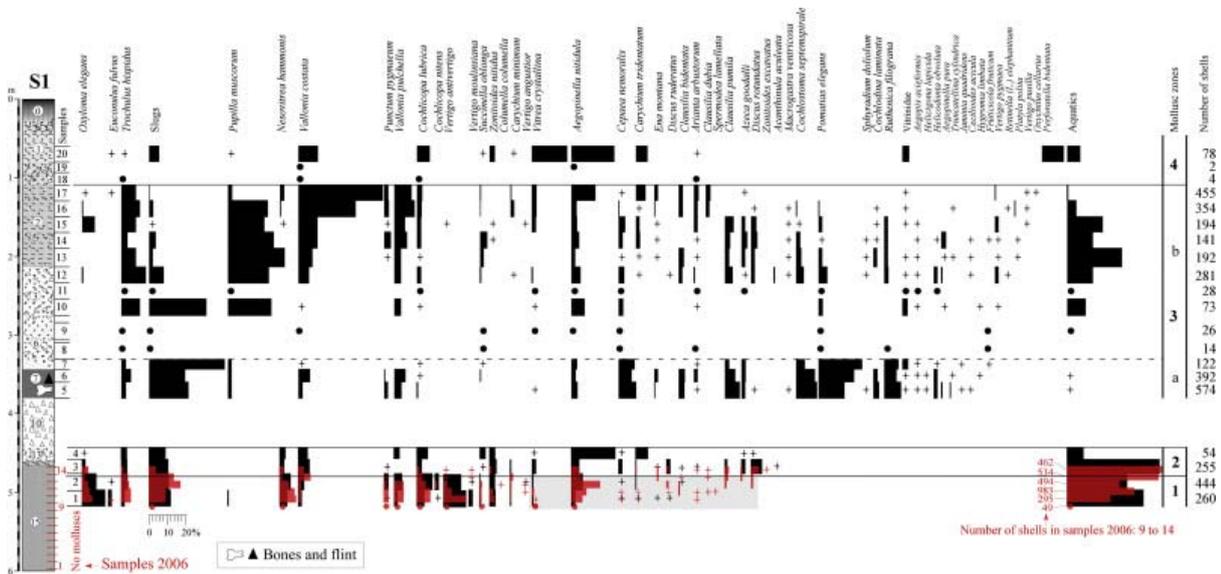
Fig. 4. Mollusc diagrams from La Celle sections Cp2 and Cp1. The upper part of Cp1 is reworked and yielded disturbed contaminated assemblages poor in species and shells (see keys on Fig. 3 and lithology on Fig. 2).



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Fig. 5. Mollusc diagram from La Celle profile S5 (see keys on Fig. 3 and lithology on Fig. 2).



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Fig. 6. Mollusc diagram from La Celle profile S1 (see keys on Fig. 3 and lithology on Fig. 2).

### 3.1.1. Biozone 1: Damp open-ground assemblage

This zone is identified in the basal units (Fig. 3: S2, unit 14, samples 21–24; Fig. 4: Cp2, unit 14, samples 1–4; Fig. 6: S1 unit 15, samples 1–2 and 6.09–6.12). In the upper part of the slope where the tufa lies directly on the calcareous bedrock, zone 1 is recognized within a fine silty tufa (unit 14). Molluscan assemblages comprise a range of ecologically tolerant species (*Cochlicopa lubrica*, *Vallonia pulchella*, *Trochulus hispidus*, *Nesovitrea hammonis*, *Punctum pygmaeum*, *Euconulus fulvus*) and those characteristic of wetlands (*Oxyloma elegans*, *Zonitoides nitidus*). Several strictly hygrophiles (*Vertigo antivertigo*, *Vertigo genesii*, *Vertigo geyeri*) are restricted to this zone. The last two are noteworthy for having North European and Alpine modern ranges (Welter-Schultès, 2012), and were part of the regional interstadial pioneer fauna of the Weichselian Lateglacial (Limondin-Lozouet, 2011). These assemblages indicate a wet and open habitat, a conclusion supported by the complete lack of shade-demanding taxa.

In the basal part of the slope, the earliest malacological communities were recovered from a fluvial silt (unit 15) underlying the basal tufa previously described as unit 14. Molluscs are dominated by aquatic taxa, which represent half of the molluscan population (Fig. 6). The terrestrial component is similar to that of unit 14 with tolerant species, strict hygrophiles and a few boreo-alpine species (*Cochlicopa nitens*, *Columella columella*). However, it also includes a number of shade-demanding species that characterize closed environments. Two taxa (*Vitrea crystallina*, *Aegopinella nitidula*) are relatively well represented although most of these shade-demanding species occur as single shells. The occurrence of these woodland snails is ecologically incompatible with the dominant species of the assemblage which inhabit damp open-ground. Moreover, they are completely absent in the assemblages recovered from the overlying tufa (unit 14) formed from springs upslope. These species, highlighted in grey on the diagram (Fig. 6), are likely to be intrusive from the uppermost unit 13 tufa deposit directly overlying level 15 at this location.

Environmental conditions reflected by zone 1 faunas can be described as marshy grassland. Among boreo-alpine species, some are glacial relics (*C. columella*) and several are characteristic of pioneer faunas of the earliest stage of malacological successions (*V. genesii*, *V. geyeri*, *C. nitens*) as already registered in the area during interstadial and/or early interglacial times (Limondin, 1995; Preece and Bridgland, 1999; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011).

### 3.1.2. Biozone 2: Expansion of forest assemblage

This zone (units 13 to 8; S2: samples 25–38, Cp1: samples 1–6, Cp2: samples 5–24, S5: samples 1–8, S1: samples 3–4 and 6.13–6.14) is characterized by a progressive marked increase in species diversity and number of shells (Fig. 3, Fig. 4, Fig. 5, Fig. 6). Most of the newcomers are shade-demanding taxa (70% of the total number of species), indicating expansion of a forest environment. This interpretation is reinforced by the replacement of the more hygrophilous open-ground species *Vallonia pulchella* by its congener *Vallonia costata*, a more shade-tolerant species better adapted to drier conditions. The

successive arrivals of forest snails make it possible to distinguish three subzones called 2a to 2c. Sampling from the top part of Cp1 was undertaken in unit 10 that was recognized as a colluvial deposit, implying that its palaeontological content might possibly be disturbed. Indeed, assemblages from this layer show dramatic decreases both in the number of shells and the diversity of species. Many of the incoming forest species in the underlying level as well as the aquatic molluscs become sporadic or disappear in unit 10 (Fig. 4). This sudden change is linked to a stratigraphic discontinuity and the impoverished assemblage appears to result entirely from reworking. Consequently, this section was considered inaccurate and samples 7 to 14 are not included in the following analyses (Fig. 4).

Subzone 2a: *Discus ruderatus* is the emblematic species of this sub-stage recognized on two profiles in unit 13 (S2 and Cp2, Fig. 3, Fig. 4). This boreo-montane snail currently lives in coniferous woods (Kerney and Cameron, 1979; Welter-Schultès, 2012) and is regularly recorded in early Holocene sequences in North-West Europe when forest cover begins to develop (e.g. Preece and Day, 1994; Preece and Bridgland, 1999; Meyrick, 2001; Coutard et al., 2010; Limondin-Lozouet and Preece, 2014). At La Celle, it is accompanied by a diverse group of forest snails which however represent less than 10% of the total land snails. Ecologically, these early colonizers are among the most tolerant in the shade-demanding category (*Vitrea crystallina*, *Clausilia bidentata*, *Ena montana*, *Spermodea lamellata*, *Zonitoides excavatus*) and some of them are known to prefer low density woods (*Aegopinella nitidula*, *Cepaea nemoralis*, *Azeca goodalli*). This first forest assemblage represents a pioneering stage in the development of tree cover including coniferous species.

Subzone 2b is defined by the appearance of *Discus rotundatus*, a common European forest snail whose current distribution is wide but limited northward to southern Scandinavia (units 12 and 11, S2, Cp2, S5, Fig. 3, Fig. 4, Fig. 5). In the sequences of the study area, the replacement of *D. ruderatus* by *D. rotundatus* is a characteristic feature of the early part of interglacials (Limondin-Lozouet, 2011). Based on comparison with pollen data in the Holocene, the development of *D. rotundatus* has been linked with the establishment of deciduous forest (Preece and Day, 1994; Preece and Bridgland, 1999; Meyrick, 2001; Limondin-Lozouet et al., 2005). The development of a denser tree canopy is reflected by the increasing number of shade-demanding snails, which make up to 20–30% of the total number of individuals. *Carychium tridentatum*, typical of moist forest soils, expands significantly. Among newcomers, members of the Clausiliidae are diversified. *Clausilia dubia*, a Central European species, more common in moist rocky habitats than in woodlands (Horsák et al., 2013), occurs specifically this time whereas most representatives of this family are obligate forest snails (*Clausilia pumila*, *Cochlodina laminata*, *Macrogastra ventricosa*).

Subzone 2c, observed in units 9 and 8 (S2, Cp2, S5, Fig. 3, Fig. 4, Fig. 5), can be named after *Retinella (Lyrodiscus) elephantium*, the emblematic species of MIS 11 malacofaunas in north-western Europe. This zone is characterized by the appearance of several species of moist closed canopy woodland (*Retinella elephantium*, *Balea heydeni*, *Platyla polita*, *Fruticicola fruticum*, *Aegopinella pura*, *Helicodonta obvolvata*, *Oxychilus navarricus*) whereas more tolerant species, such as *C. dubia*, decline. Proportions of forest snails became stabilized with a mean value of about 30% although in some samples, they can represent up to 46% of the total number of shells. At this stage the forest cover has increased in density.

### 3.1.3. Biozone 3: Maximum diversity of forest assemblage

During this episode forest snails experienced a new increase in diversity, reaching 28 species (units 7 to 2; S2: samples 39–41, Cp2: samples BS4–BS3, S5: samples 9–22, S1: samples 5–17). All these last newcomers have modern distributions covering the Mediterranean area but hardly extend northwards beyond 55° latitude (*Ruthenica filigrana*, *Pomatias elegans*, *Cochlostoma septemspirale*, *Sphyradium doliolum*, *Pagodulina pagodula*, *Aegopis acieformis*, *Platyla similis*). Their presence indicates particularly mild conditions and most of them are typical of a closed canopy. However, fluctuations in the number of shells together with the sharp development of certain taxa lead to the distinction of two subzones labelled 3a and 3b.

Subzone 3a relates to the assemblages with the highest proportion of forest snails (50–70%) from the entire sequence. They are characterized by the appearance of three calcicolous species (*P. elegans*, *R. filigrana*, *C. septemspirale*) which show their maximum development. Subzone 3a is interpreted as reflecting maximum density of the forest cover. These assemblages are identified in level 7 in profiles S1 and S5 (Fig. 5, Fig. 6) and also in level 4 in profile Cp2 (Fig. 4), suggesting a correlation between both stratigraphic units.

Subzone 3b extends from units 6 to 2 (Fig. 5, Fig. 6). Diversity of forest snails is maintained, but the number of individuals from this category fluctuates and tends to decrease. At the same time, several taxa of open environments (*Trochulus hispidus*, *Pupilla muscorum*, *V. costata*) that have almost disappeared from the previous subzone become more common. *Vallonia costata* increases markedly at the top of the subzone in level 2, where the proportion of forest snails is lowest, with average values reaching only 17%. Interestingly the mesophilous *C. dubia* reappears during this phase. These assemblages indicate a less dense forest cover interrupted by open areas of herbaceous vegetation that create a mosaic

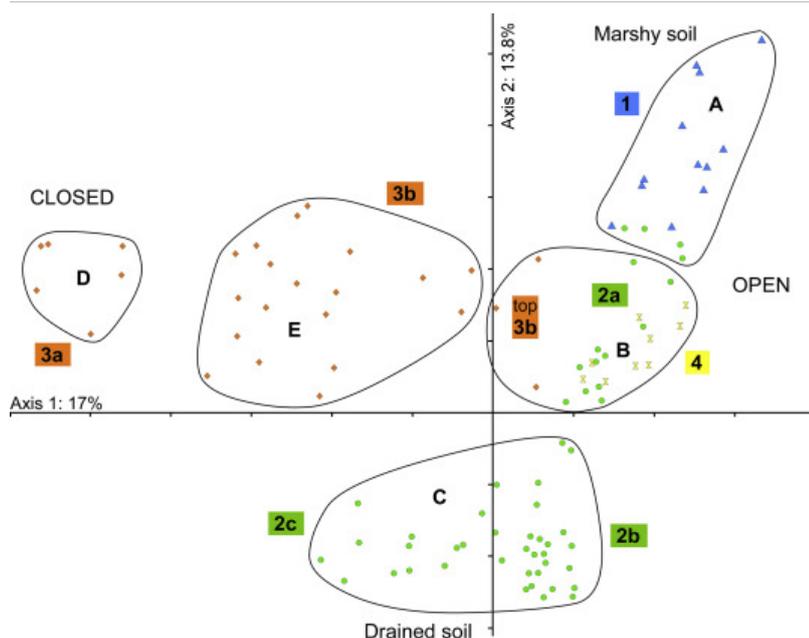
landscape.

### 3.1.4. Biozone 4: Decline of forest assemblage

This zone is recognized in the upper sandy tufa of unit 1 (S5: samples 23–30, S1: samples 18–20). The malacofaunas are very different from the earlier assemblages. Most of the strict forest species have disappeared, leaving an assemblage of shade-demanding taxa (*A. nitidula*, *V. crystallina*, *A. arbustorum*) less strongly tied to this habitat and similar to that present in zone 2, at the beginning of forest expansion. They are accompanied by some more specialized taxa from very wet woodlands such as *S. lamellata*, *O. navarricus* and *Perforatella bidentata*, the latter appearing for the first time in the succession. The dominant snails in this episode are hygrophilous open-ground taxa (*Oxyloma elegans*, *Succinella oblonga*, *T. hispidus*, *V. costata*). These assemblages reflect wet, largely open habitat with some humid woodland.

## 3.2. Multivariate analyses: The palaeoecological categories

The molluscan data-set was studied using numerical methods to test the robustness of the proposed biostratigraphical divisions and to assist in addition palaeoecological interpretation. Statistical processing followed the recommendations applied to malacological data, i.e. correspondence analysis coupled with cluster analysis (Rousseau et al., 1991). Aquatic taxa have been grouped under a single category while reworked samples (upper part of Cp 1) and impoverished assemblages (under 50 shells) were excluded: the analysed data-set thus comprised 101 samples and 73 taxa. The numbers of shells were coded into abundance classes on a logarithmic scale to reduce large differences in species representation. The first two axes of the correspondence analysis explain 30,92% of the total variance of the cloud (Fig. 7). If all the assemblages and the taxa explained the total information in the same way, their contribution to this explanation would be 1/101 (1%) and 1/73 (1,4%) respectively, which is actually never the case. Thus, all the assemblages or taxa that indicate a value above the respective thresholds contribute significantly to the construction of the cloud plot and are taken into account to explain the distribution of the different elements on the axes (Table 2).



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Fig. 7. Correspondence analysis (CA) undertaken on the complete malacological data-set from La Celle. Biostratigraphical zones 1 to 4 are identified by the corresponding samples shown as follows: zone 1 blue triangles; zone 2 green dots; zone 3 orange diamonds; zone 4 yellow crosses. The CA allows the classification of the malacological assemblages into five categories (A to E) related to extent of shading (Axis 1) and humidity (Axis 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2. Correspondence analysis of the malacological samples from La Celle. Significant contributions, greater than the theoretical thresholds of species (1,4%) and samples (1%) explain the variability of the data-set according to the first two axes. Positive (blue) and negative (yellow) signs indicate the location on the axes.

Species	Axis 1 %	Axis 2 %	Samples	Axis 1 %	Axis 2 %
<i>Pomatias elegans</i>	- 12.153	+ 3.602	S5 10	- 14.074	+ 1.288
<i>Cochlostoma septemspirale</i>	- 10.52	+ 3.038	Cp2 BS4	- 8.549	+ 1.456
<i>Ruthenica filograna</i>	- 9.473	+ 2.482	S1 5	- 6.988	+ 1.205
<i>Helicodonta obvoluta</i>	- 4.802		S1 6	- 5.933	+ 1.512
<i>Cochlodina laminata</i>	- 4.767		S1 7	- 3.682	
<i>Pupilla muscorum</i>	- 3.479		S5 14	- 2.326	
<i>Sphyradium doliolum</i>	- 3.243		S1 12	- 2.283	+ 1.436
<i>Truncatellina cylindrica</i>	- 2.479		S5 12	- 1.831	
<i>Aegopsis acieformis</i>	- 2.079		S2 39	- 1.728	
<i>Cepaea nemoralis</i>	- 2.076		S1 13	- 1.401	
<i>Vallonia excentrica</i>	- 1.981		S5 17	- 1.232	
<i>Pagodulina pagodula</i>	- 1.967		S5 11	- 1.176	
<i>Clausilia pumila</i>	- 1.36		S2 36	- 1.042	
			Cp2 BS3	- 1.032	
<i>Oxyloma elegans</i>	+ 3.932	+ 3.34	S5 15	- 1.003	+ 1.287
<i>Vertigo antivertigo</i>	+ 3.831	+ 7.424			
<i>Zonitoides nitidus</i>	+ 2.908	+ 2.44	S1 6.11	+ 2.393	+ 3.375
<i>Nesovitrea hammonis</i>	+ 2.65		Cp1 1	+ 2.017	+ 1.678
<i>Carychium minimum</i>	+ 2.346	+ 3.084	S1 2	+ 1.792	
Aquatics	+ 2.217	+ 7.386	S2 24	+ 1.562	+ 3.772
<i>Succinella oblonga</i>	+ 1.628		S1 1	+ 1.559	
<i>Euconulus fulvus</i>	+ 1.363		Cp1 2	+ 1.68	+ 1.705
<i>Vallonia pulchella</i>		+ 13.766	S1 6.10	+ 1.471	+ 2.691
<i>Clausilia sp.</i>		+ 2.077	S1 6.12	+ 1.433	+ 1.945
			Cp1 3	+ 1.288	
<i>Acanthinula aculeata</i>	- 4.988		S5 29	+ 1.249	
<i>Discus ruderatus</i>	- 4.617		S5 28	+ 1.078	
<i>Carychium tridentatum</i>	- 4.198		S2 23		+ 3.105
<i>Azeqa goodalli</i>	- 3.445		S2 22		+ 3.079
<i>Ena montana</i>	- 3.425		Cp2 4		+ 1.546
<i>Clausilia bidentata</i>	- 3.414		Cp2 5		+ 1.531
<i>Columella edentula</i>	- 2.954				
<i>Vitrea contracta</i>	- 2.552		Cp2 12		- 2.915
<i>Vertigo pusilla</i>	- 2.439		Cp2 13		- 2.746
<i>Discus rotundatus</i>	- 1.914		Cp2 11		- 2.452
<i>Zonitoides excavatus</i>	- 1.887		Cp2 14		- 2.427
<i>Lauria cylindracea</i>	- 1.474		Cp2 17		- 2.015
			Cp2 10		- 1.917
			Cp2 15		- 1.867
			Cp2 21		- 1.719
			S2 30		- 1.581
			S2 33		- 1.421
			S5 4		- 1.393
			S2 34		- 1.353
			S5 3		- 1.347
			S2 29		- 1.261
			Cp2 22		- 1.203
			N12		- 1.191
			Cp2 20		- 1.149
			S2 32		- 1.096
			S5 8		- 1.095
			Cp2 19		- 1.066
			Cp2 23		- 1.065
			S2 38		- 1.062
			Cp2 18		- 1.05
			S2 35		- 1.047
			Cp2 9		- 1.046
			Cp2 24		- 1.001

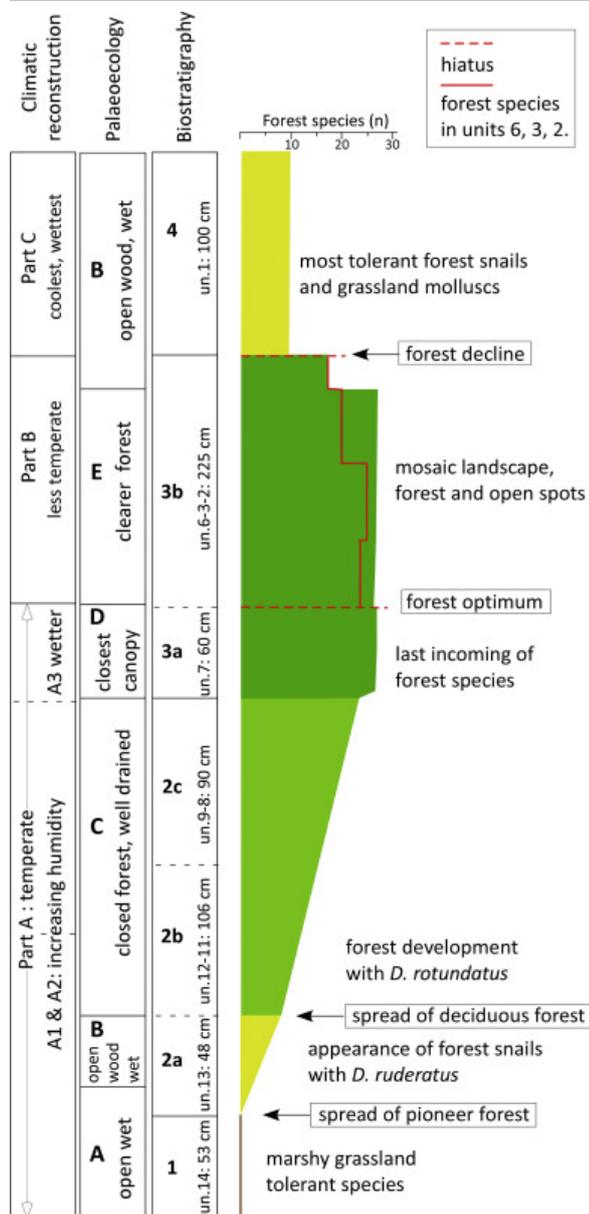
The first axis (Fig. 7, Table 2) discriminates shade-loving species on its negative pole (e.g. *P. elegans*, *C. septemspirale*, *R. filograna*, *H. obvoluta*, *C. laminata*) and open habitat taxa on the positive side (e.g. *O. elegans*, *V. antivertigo*, *Z. nitidus*). The assemblages indicating a high negative contribution to the variance come from the fine grey tufa unit 7, corresponding to the maximum development of the forest cover. Those with positive values originate from both basal (units 15 and 14) and upper (unit 1) levels yielding assemblages of the most open environments with no or very few shade-loving snails.

Strictly hygrophiles (e.g. *V. pulchella*, *V. antivertigo*, Aquatics, *O. elegans*, *C. minimum*, *Z. nitidus*), combined with some forest snails (*P. elegans*, *C. septemspirale*, *R. filograna*), characterize the positive pole of axis 2. At the negative pole are grouped forest habitat species (e.g. *A. aculeata*, *D. ruderatus*, *C. tridentatum*, *A. goodalli*, etc.). The corresponding assemblages on the positive side come from basal levels 15 and 14, indicating marshy biotopes. At the negative pole of axis 2 are many samples from the lower half of the tufa (units 13 to 8) with malacofaunas reflecting forest development. Axis 2 therefore opposes marshy environments to well-drained soil habitats.

Sets A to E, drawn on the projection of the first factorial plane (Fig. 7), were defined according to an ascendant hierarchical classification using the Euclidian distance, grouping together assemblages having great similarities in their qualitative and quantitative composition (Fig. S1: in supplementary data). These categories which correspond to palaeoecological conditions, are compared with biostratigraphical zones on Fig. 7. Group A isolates faunas of wet marshy environments and is essentially equivalent to Biozone 1. Group B consists of malacofaunas representative of humid habitats, essentially open but including a small proportion of closed habitat species. The corresponding biotopes can be described as mosaics, open spaces with wooded areas. In the biostratigraphical succession, this type of environment is identified at the beginning of forest expansion (Subzone 2a) and at the top of the series, when forest cover begins to decline (top of Biozone 3) before decreasing sharply (Biozone 4). The third category C concerns assemblages grouped at the negative pole of axis 2 and equates with Subzones 2b and 2c, the first is represented on the positive side of axis 1 and the second subgroup is located on the negative side, indicating the development of closed canopy. Group D includes all the samples with the highest proportions of forest snails and is equivalent to Subzone 3a, corresponding to the maximum density of the forest cover. In the last category E, are most of the samples of Subzone 3b, characterized by a community of forest snails highly diversified but showing a declining number of individuals.

### 3.3. Synthesis and discussion of the palaeoenvironmental and climatic succession at La Celle

The statistical analyses of the malacological succession at La Celle can now be compared with the results of stable isotope and trace element analyses on tufa calcite to investigate common trends that might be caused by climate (temperature and humidity) as opposed to other factors (Dabkowski et al., 2012). Moreover, comparison of La Celle malacological results with the well-known regional Lateglacial-Holocene molluscan succession (Preece and Bridgland, 1999; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011) and discussion of the data obtained versus the scheme of forest dynamics established by palynologists for temperate Europe (van der Hammen et al., 1971; De Beaulieu et al., 2006; Birks and Tinner, 2016) help to identify several important thresholds in the vegetation evolution in the succession (Fig. 8).



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Fig. 8. Vegetational development at La Celle during MIS 11 based on molluscan data. Distribution of forest species and biozones are plotted against climatic episodes inferred from the geochemical record of tufa calcite (Dabkowski et al., 2012).

The earliest part of the sequence reflects the development of a marshy grassland (Biozone 1). Assemblages include tolerant taxa persistent from earlier cold faunas (*O. elegans*, *T. hispidus*, *P. muscorum*) together with some pioneer species with northern modern ranges that are known in the area during the Lateglacial (*C. nitens*, *V. genesii*). Improvement of climatic conditions is also reflected by the occurrence of more thermophilous molluscs of grassy habitats. In north-western Europe early malacological recolonization of floodplains is characterized by assemblages composed of ecologically tolerant species, usually of marshland (e.g. Preece and Bridgland, 1999; Limondin-Lozouet and Preece, 2004). Parallels can be seen with the assemblages dated from the Lateglacial interstadial and/or the very beginning of the Holocene, indicating the first stage of climatic improvement (Preece and Robinson, 1984; Preece et al., 1995; Limondin-Lozouet and Antoine, 2001; Limondin-Lozouet, 2011).

The appearance of the first forest taxa indicates the spread of pioneer forest. Although assemblages will diversify rapidly, the very beginning of this phase at La Celle was still dominated by species reflecting an open landscape (Fig. 8: end of ecological zone A). Forest snails occurring during this episode are among the most tolerant in this category (Fig. 8: Biozone 2a). Many of them have current distributions extending northwards into Scandinavia and several are abundant in open woods and coniferous forest (e.g. *D. ruderatus*, *V. crystallina*, *A. nitidula*, *C. bidentata*). Climatic conditions revealed by

the isotopic record indicate interglacial temperatures and increasing humidity. This early stage of forest development appears to relate to the *Pinus-Betula* phase at the beginning of interglacial cycles shown by pollen data across Europe (van der Hammen et al., 1971; Birks and Tinner, 2016).

During the diversification of shade-loving species that defines Biozone 2, the appearance of *Discus rotundatus* is thought to reflect the spread of deciduous forest. The replacement of the boreo-montane *D. ruderatus* by *D. rotundatus*, a species with a southernmost modern range, is well known in Holocene sequences where it coincided with the expansion of *Corylus* (Preece and Day, 1994; Preece and Bridgland, 1999; Meyrick, 2001; Limondin-Lozouet et al., 2005). A similar replacement has also been observed at the beginning of the Eemian interglacial succession in the area (Limondin-Lozouet, 2011). In the pollen reference succession of the MIS 11 Praclaux interglacial, the expansion of *Corylus* marks the development of deciduous forest (De Beaulieu et al., 2006).

At La Celle, the acme of forest development is reached in ecological zone D characterized by the final arrival of forest species and the greatest richness of forest snails (Biozone 3a, Tables S1 to S5) with modern distributions mostly southern Europe and never reaching as far north as Scandinavia. According to climatic reconstructions derived from geochemical data at La Celle this episode of closest canopy is the wettest of the most temperate period and is interpreted as the climatic optimum phase (Dabkowski et al., 2012).

The diversity of forest snails remained similar in Biozone 3b but, occurrence of shade-loving taxa was not continuous within the stratigraphical sequence. Species occurrences during this episode are very variable (Fig. 8: red line). At least two peaks of open-ground land snails (*P. muscorum*, *V. costata*) occurred during Biozone 3b (Fig. 5, Fig. 6), reflecting a dynamic mosaic landscape involving episodes of forest interspersed with phases with more open conditions (ecological zone E). The geochemical record from La Celle suggests that this dynamic episode coincided with a period of decreased temperatures with several short dry oscillations (Part B: Fig. 8; Dabkowski et al., 2012). Major disruptions in the land snails populations and sharp inflections in the geochemical record (Dabkowski et al., 2012) at both the onset and end of Biozone 3b (Fig. 5, Fig. 6) almost certainly relate to hiatuses in the record resulting from erosion on the slope (Fig. 8: dotted red lines).

In the upper part of the succession, forest recession is reflected by a marked decrease in the frequency of shade-loving snails, which falls by two thirds (Fig. 8: Biozone 4). All highly specialized forest snails disappeared and the remaining species in this category (*E. montana*, *A. arbustorum*, *V. crystallina*) are the most tolerant of lower temperatures, often inhabiting montane regions and with modern distributions extending into northern Europe. In addition, several hygrophilous taxa of open habitat (*O. elegans*, *T. hispidus*) or humid forest (*S. lamellata*, *P. bidentata*) also occurred. Environmental conditions reflected by mollusc assemblages are similar to those prevailing at the very beginning of the forest expansion corresponding to palaeoecological category B (Fig. 8). The landscape was generally open with dense herbaceous cover providing various humid habitats around bushes and trees. The malacological data are consistent with the isotopic records that indicate that this period had the coolest and wettest conditions in the entire sequence (Fig. 8: Part C), but still falling within the range of interglacial conditions (Dabkowski et al., 2012). This period might correspond either to the final phase of deciduous forest characterized by a decrease of arboreal pollen (AP) and spread of hygrophilous taxa (*Carpinus*, *Fagus*, *Abies*) or, to the humid boreal forest (*Picea*, *Pinus*, *Betula*) that develops at the very end of interglacials (van der Hammen et al., 1971; De Beaulieu et al., 2006; Birks and Tinner, 2016). Both hypotheses imply woodland dominated by trees producing unfavourable leaf-litter for molluscan populations (*Carpinus* and *Fagus* in hypothesis 1 or coniferous taxa in hypothesis 2). Indeed less accessible citrate calcium in leaf-litter can severely impact diversity and richness of molluscan assemblages, such as those that existed across Europe during the early Holocene when deciduous forest replaced coniferous woodland as reflected by the appearance of the most shade-demanding forest snails (Horsák et al., 2020). At La Celle the marked decrease in diversity observed at the top of the sequence is thought to result from a replacement of deciduous forest by open woodland. The sharp decrease in the frequency of forest snail and the abrupt change to cooler and wetter conditions, at the boundary between stratigraphic units 2 and 1, is likely to result from a sedimentary hiatus; in this case, both explanations are possible.

In the stratigraphical context of La Celle, the earliest malacofaunas of the succession showing the typical characteristics of early temperate phase pioneer assemblages (Biozones 1 and 2a) come from fine silty layers (units 14 and 13) overlying coarser sand and basal gravel deposits of the fluvial succession. These finer sediments accumulated at the beginning of a temperate period as demonstrated in the climato-sedimentary scheme of the regional terrace system (Antoine et al., 2000). This change in the sedimentary facies, well known from the transition between the Weichselian and Holocene in Northern France, corresponds to a change from a periglacial braided-river system, depositing coarse gravels and sand bars on the whole alluvial plain, to a meandering river confined to a single channel in which calcareous overbank silts are deposited during flooding events (Antoine, 1997; Antoine et al., 2003a, Antoine et al., 2003b). Both faunal and lithological

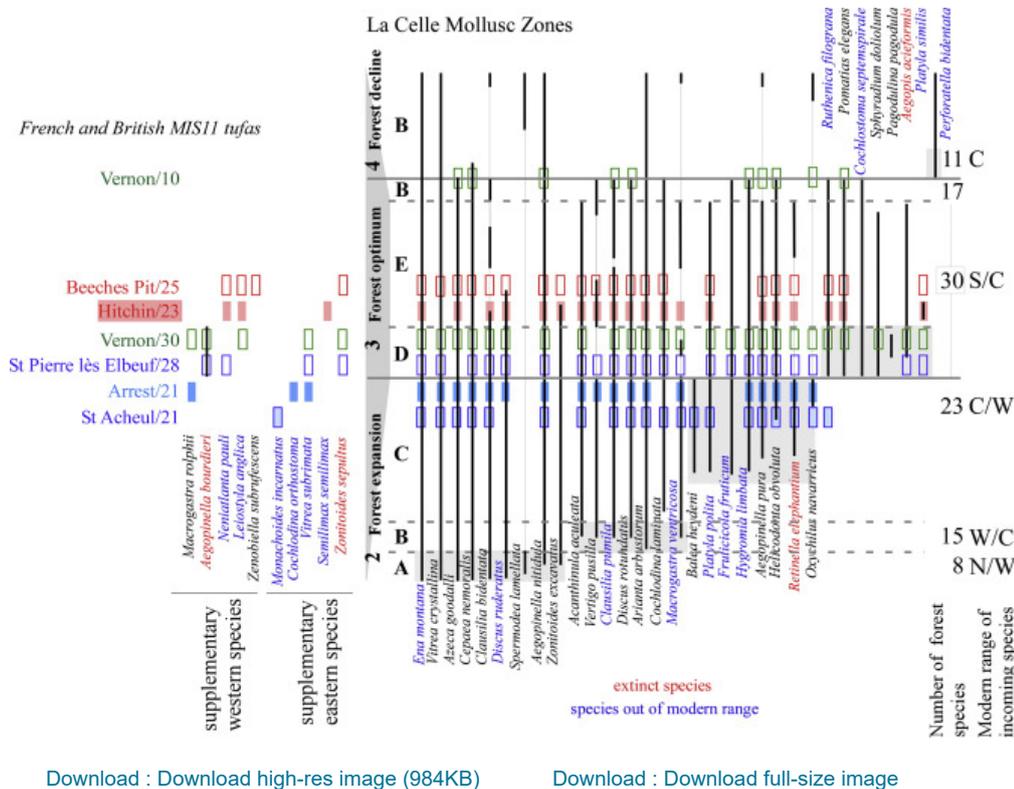
observations thus favour a position of Biozones 1 and 2a of La Celle sequence (Fig. 8) at the beginning of the interglacial. Subsequently forest faunas became established as temperatures increased, suggesting that this early part of La Celle record (Biozones 2b and 2c) equates with the spread of temperate forest that began in Europe from 430 / 415 ka (De Beaulieu et al., 2006; Desprat, 2007; Koutsodendris et al., 2010). The maximum peak in land snail richness and diversity is reached within units 7 and 4 that yielded similar assemblages (ecological zone D and Biozone 3a). This period is the warmest registered in the isotopic record at La Celle and is likely to correspond to the MIS 11c thermal optimum, which has been recorded around 404–406 ka in marine and ice cores (Imbrie et al., 1984; EPICA Community members, 2004). This correlation is consistent with dates around 400 ka obtained at La Celle (Table 1) and the age of the *Lyrodiscus* assemblage from Beeches Pit in Britain, similarly dated to about 450 ka and correlated with the late temperate stage (Ho III) of the Hoxnian, allocated to MIS 11c (Preece et al., 2007). During the following Biozone 3b/ecological zone E, the land snail assemblages indicate a less dense forest cover culminating in those from Biozone 4 that suggest open woodland, whereas the geochemical records indicate a general cooling interrupted by hiatuses at the onset of each episode of forest decrease (Fig. 8). Parts B and C of the geochemical records appear to coincide with periods of forest regression observed in high resolution pollen sequences and with abrupt changes in Northern Atlantic circulation (Dabkowski et al., 2012).

#### 4. Comparisons and discussion on NW European mollusc recolonization during MIS11

The statistical analyses carried out on the malacological data from La Celle have allowed the recognition of changes in assemblages over time (Biozones) and the definition of biotopes that relate to particular climatic contexts (Ecological Zones). These analyses help to characterize different stages of forest development. Forest species are the specific signature of interglacial assemblages (e.g. Mania, 1995a; Preece, 1997; Ložek, 2000). Furthermore, studies of European interglacial malacofaunas show that the order of arrival of particular species is often related to their modern geographical range, which helps to pinpoint the location of possible refugia (Ložek, 2000; Limondin-Lozouet and Preece, 2014). The following discussion reviews these issues with respect to the long succession of La Celle, which is used as a model against which to compare other malacological records of MIS 11 age from northern Europe.

##### 4.1. Placing the “*Lyrodiscus* fauna” within MIS 11 molluscan successions from NW Europe

The so-called “*Lyrodiscus* assemblage” has been recognized as a malacological signature of MIS 11 across NW Europe (Rousseau et al., 1992; Rousseau, 2003; Preece et al., 2007; Limondin-Lozouet and Antoine, 2006; Cliquet et al., 2009; Limondin-Lozouet, 2017). It includes a group of extinct species together with allochthonous snails, now living in Central and Southern Europe. This assemblage had a diverse biogeographical group composition that has no modern counterpart. It has been recovered only from tufa deposits and has led to the recognition of a peculiar humid forest environment that existed during the climatic optimum of the interglacial. Recently, new malacological data and reappraisal of old collections have produced improved lists of species from the MIS 11 localities and a taxonomic reassessment of the *Lyrodiscus* species. This study demonstrated that the species after which the assemblage is named is *Retinella (Lyrodiscus) elephantium* (=skertchlyi) and that the assemblage is restricted to Western Europe (Limondin-Lozouet and Antoine, 2006). However, most of the relevant sequences are incomplete and provide only short records of the faunal succession. The sequence from La Celle has the longest and most detailed record of the forest expansion during the MIS 11 interglacial showing how the *Lyrodiscus* assemblage developed and enabling it to be put into context. The mollusc succession of La Celle therefore provides a framework within which the order of arrival of forest species can be established and the development of diversity demonstrated (Fig. 9). The appearance of new arrivals happened regularly during the development of forest until the optimum, after which diversity decreased and, with the exception of *P. bidentata* that occurs in the upper part, no additional forest species is recorded. The modern distribution of species indicates a malacological recolonization from west to east during the expansion of forest, which culminated with the arrival of southern species during the optimum. Six other MIS 11 tufa sequences yielding a *Lyrodiscus* assemblage have been identified in northern France (Rousseau et al., 1992; Limondin-Lozouet and Antoine, 2006) and south-east England (Kerney, 1959; Preece et al., 2007) (Fig. 1).



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Fig. 9. Zonation of the MIS 11 forest malacofaunas in North-West Europe based on the succession at La Celle.

The diagram shows the presence of forest species at La Celle (black lines). Mollusc zones are indicated according to biostratigraphic divisions (2 to 4) and palaeoecological groups (A to E) previously defined at La Celle (Fig. 7). The arrival of new groups of forest species is highlighted in grey and the modern European ranges are indicated (N: North, W: West, C: Centre, S: South). The number of species is given for each palaeoecological episode. The occurrence of forest species in the other MIS 11 tufa sequences are indicated by coloured squares lines in front of the site name and number of species. The record from the tufa at Vernon is divided into lower and upper levels. Forest snails occurring in neighbouring sequences, but not at La Celle, are mentioned as “supplementary species” and are classified according to their modern range into a western and an eastern group. Species occurring beyond their modern ranges are in blue and extinct taxa are in red. The possible occurrence of the extinct species *Aegopinella bourdieri* at La Celle has been checked by evaluation of specimens in old collections; it was not recovered in recent samples, its position in the succession is assumed from the presence of the taxon in the other localities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

At Vernon in the Seine valley, the observed tufa was 2,5 m thick and yielded malacological assemblages split into two biostratigraphical zones reflecting a dense forest phase followed by an episode of decreased tree cover (Rousseau et al., 1992). None of the other calcareous deposits exceed one metre in thickness and contain similar molluscan assemblages, reflecting closed forest. Records from these six sites are plotted against the more complete succession from La Celle according to both levels of diversity and common occurrences of forest species. Forest snails absent from La Celle are mentioned as supplementary species and grouped by their geographical ranges (Fig. 9). The Saint Acheul and Arrest forest assemblages appear to relate to ecological zone C at La Celle when the deciduous forest had become established but had not yet reached its maximum diversity. Hitchin, Beeches Pit, Saint Pierre-lès-Elbeuf and the lower tufa at Vernon all yielded rich molluscan assemblages including species with Southern European modern ranges, which correspond to the most diverse assemblages at La Celle (Biozone 3). This forest optimum phase is characterized by a number of species, some now extinct, that are otherwise rare or unknown from other Pleistocene interglacials (Fig. 9). These species include *Neniatlanta pauli*, *P. similis*, *Aegopinella bourdieri*, *A. acieformis*, *R. filograna*, *Zonitoides sepultus*. However, the temporal resolution of the tufa sequences is not good enough to shed light on their order of arrival. These assemblages at St Pierre-lès-Elbeuf and Vernon are equated with ecological zone D at La Celle because of their high diversity (Fig. 9). The placement of the molluscan assemblages from Hitchin and Beeches Pit within the framework of La Celle is a matter of debate. Their lower diversity could be interpreted as reflecting the initial opening up of closed canopy forest, identified at La Celle succession in ecological zone E during the second part of the optimum. However, it could also be argued that the

relative impoverishment of the British sites result from their more western location and greater distance from glacial refugia. In this case a correlation with ecological zone D, rather than zone E, might be possible. Indeed, comparison of forest assemblages from Holocene tufas of Western Europe showed a trend towards reduced diversity at British sites (Limondin-Lozouet and Preece, 2014).

Finally, the upper part of the Vernon sequence has impoverished forest faunas that are comparable with those of the last division of the La Celle succession (Biozone 4 and ecological zone B) reflecting a dramatic decline of forest (Fig. 9).

#### 4.2. MIS 11 molluscan recolonization across Europe: Inferring location of glacial refugia and palaeobiodiversity

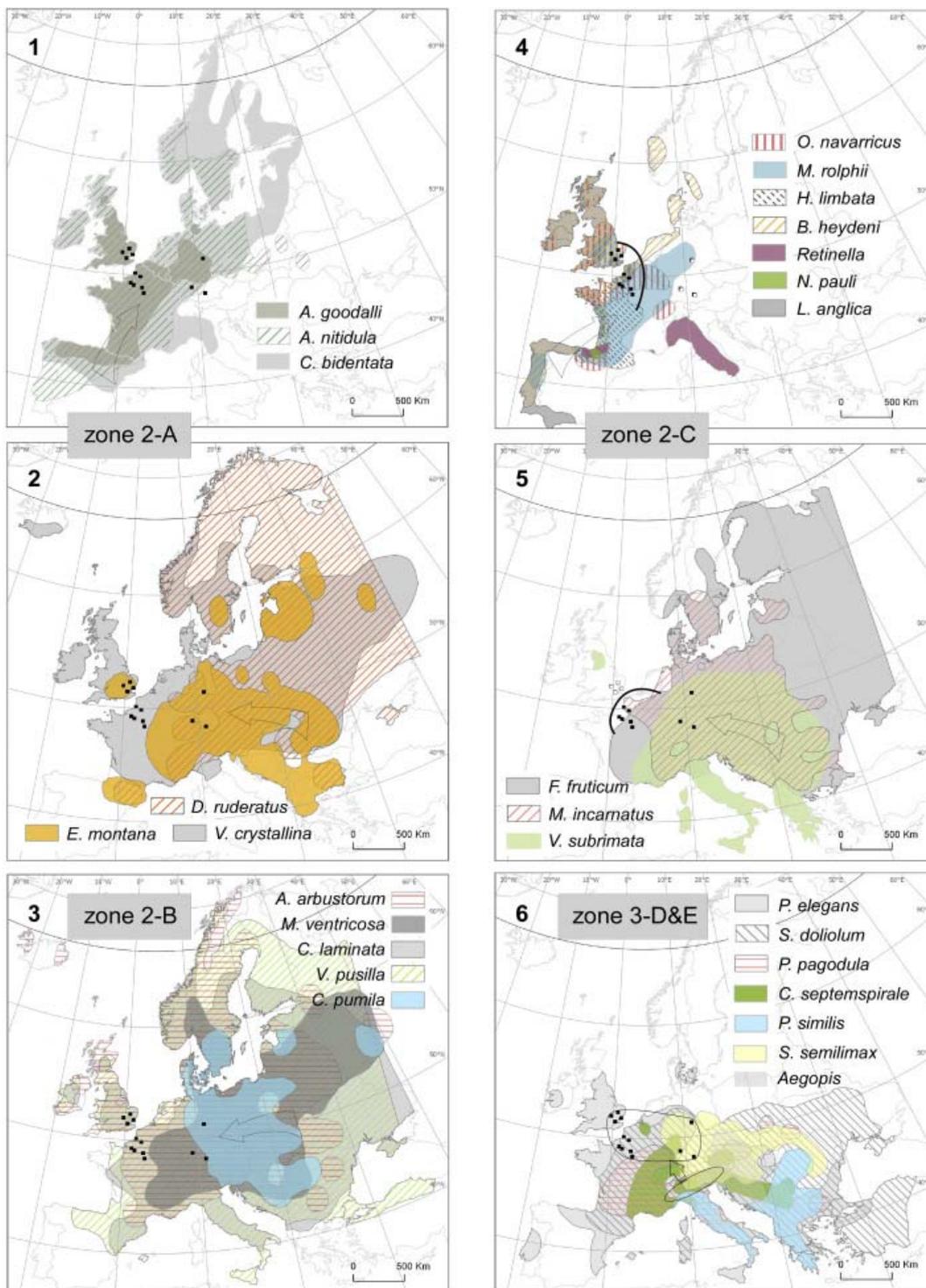
Earlier studies of Quaternary European malacofaunas emphasized important variations in the distribution areas of forest species during interglacial periods, suggesting differences in the location of refugia from which forest snails recolonized northern Europe (e.g. Puisségur, 1976; Preece, 1991; Mania, 1995a; Ložek, 2000). Moreover, detailed malacological successions show that the order of arrival of forest species is linked to the distance from refugial areas (Limondin-Lozouet and Preece, 2014; Horsák et al., 2019). Reconstruction of the history of forest snails provides clues on the possible routes of recolonization. At La Celle, the forest snail succession details the progressive development of the *Lyrodiscus* fauna allowing the reconstruction of malacological recolonization in western Europe during MIS 11 (Fig. 9).

According to the pattern identified at La Celle and other MIS 11 tufas localities, occurrences of forest snails in North-west Europe during MIS 11 are compared in all contemporaneous successions over Britain, France and Germany (Fig. 1). To the tufa formations previously mentioned, can be added the fluvial sites of Chelles (Breuil, 1939) in France, as well as Clacton (Bridgland et al., 1999) and Swanscombe (Kerney, 1971) in England. In Germany three tufa deposits are relevant: Schmiechen (Dehm, 1951), Cannstadt (von Sandberger, 1870-1875) and Bilzingsleben (Mania, 1995b; Mania et al., 2001). The occurrence of forest snails at each of the sites is recorded in relation to their pattern of occurrence at La Celle (Table 3) and for each stage of recolonization, maps of modern ranges are plotted for certain critical species (Fig. 10). Several were not selected for mapping according to three criteria (white boxes in Table 3). In the first category are species with large European distribution. Location of their refugial zones during Pleniglacial times is difficult to infer and can be multiple across Europe making those species inaccurate to define migration paths. The second category concerns snails with a single occurrence, that were also considered not relevant enough to argue the pattern of the geographical extension of the species. Thirdly, extinct species cannot be the subject of a modern geographical distribution. However, when the genus to which they belonged has a limited current extension, they have been mapped, this is the case of both genus *Retinella* and *Aegopis* which appear on maps 4 and 6 respectively (Fig. 10).

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Table 3. Occurrence of forest species at the MIS 11 sites mentioned on maps 1 to 6 (Fig. 10) in relation to the zones of the La Celle forest succession. For each zone, species are arranged according to their modern European range: west (blue), east and centre (brown), south (yellow). Species remain in white blocks when their current range is broad (i.e. European). The crosses in the coloured boxes refer to the occurrences indicated on the maps, while the crosses in the white boxes refer to occurrences that are not shown.

	Great-Britain				France					Germany			
	Beeches Pit	Clacton	Hitchin	Swanscombe	Arrest	St Acheul	Vernon	St P.Elbeuf	Chelles	Celle	Bilzingsleben	Cannstadt	Schmiechen
<b>2A: pioneer forest</b>													
<i>Clausilia bidentata</i>	x		x	x	x	x	x	x		x	x		
<i>Aegopinella nitidula</i>	x		x	x	x	x	x	x	x	x		x	x
<i>Azeca goodalli</i>	x	x	x	x	x	x	x		x	x	x	x	x
<i>Cepaea nemoralis</i>	x		x	x	x	x	x	x	x	x	x	x	
<i>Spermodea lamellata</i>										x			
<i>Zonitoides excavatus</i>	x		x							x			
<i>Vitrea crystallina</i>	x	x		x	x	x	x	x		x	x	x	x
<i>Discus ruderatus</i>	x	x	x	x	x		x			x	x		
<i>Ena montana</i>	x		x	x	x	x	x	x	x	x		x	x
<b>2B: spread of deciduous forest</b>													
<i>Arianta arbustorum</i>	x		x	x	x	x	x	x	x	x	x	x	x
<i>Cochlodina laminata</i>	x		x				x	x	x	x	x	x	x
<i>Vertigo pusilla</i>	x		x	x	x		x			x	x		x
<i>Macrogastra ventricosa</i>			x	x	x	x	x	x		x		x	x
<i>Clausilia pumila</i>	x		x	x	x	x	x	x		x		x	x
<i>Acanthinula aculeata</i>	x		x	x	x	x	x	x		x			x
<i>Discus rotundatus</i>	x		x	x	x	x	x	x		x	x	x	x
<b>2C: dev. of deciduous forest</b>													
<i>Hygromia limbata</i>						x	x	x		x			
<i>Oxychilus navarricus</i>						x	x	x		x			
<i>Macrogastra rolphii</i>					x		x						
<i>Balea heydeni</i>						x							x
<i>Retinella elephantium</i> †	x		x		x	x	x	x	x	x			
<i>Neniatlanta pauli</i>	x		x						x				
<i>Leiostylia anglica</i>	x		x					x					
<i>Zenobiella subrufescens</i>	x												
<i>Fruticicola fruticum</i>							x	x		x	x	x	
<i>Monachoides incarnatus</i>							x	x			x	x	
<i>Vitrea subrimata</i>							x			x			x
<i>Platyla polita</i>	x		x			x	x	x		x	x	x	x
<i>Helicodonta obvoluta</i>	x		x			x	x	x		x	x	x	x
<i>Aegopinella pura</i>	x		x			x	x	x		x	x		x
<i>Ruthenica filograna</i>	x		x			x	x			x	x	x	x
<i>Cochlodina orthostoma</i>						x							
<b>3D&amp;E: maximum of deciduous forest</b>													
<i>Platyla similis</i>	x		x				x			x	x		x
<i>Cochlostoma septemspirale</i>										x		x	
<i>Sphyradium doliolum</i>							x			x	x	x	
<i>Pagodulina pagodula</i>										x	x		
<i>Pomatias elegans</i>	x		x				x			x			
<i>Semilimax semilimax</i>			x								x		x
<i>Zonitoides sepultus</i> †	x	x		x			x	x					
<i>Aegopis acieformis</i> †							x	x		x	x	x	x
<i>Aegopinella bourdieri</i> †							x	x		x			



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Fig. 10. Malacological recolonization of North West Europe during MIS 11, reconstructed from the model based on the forest snail succession at La Celle. At each step, maps of selected species show the modern ranges of the incoming species. Zones 2-A and 2-C are characterized by arrivals of species from both western and eastern routes that are displayed on two separated maps according to current geographical ranges. Species occurrences at the different MIS 11 sites are given in [Table 3](#) and noted on the maps as black dots for presence and white dots for absence. The area of maximum overlap of modern distributions is the Alps (map 6), whereas the area of maximum diversity has shifted northwards during MIS 11.

Maps 1 and 2 illustrate phase 2A of La Celle forest succession: early forest colonizers are present in the three considered regions during MIS 11. They are among the most tolerant and exhibit both western (Map 1) and north-eastern (Map 2) modern distributions suggesting the arrival of pioneer species from both south-west and central European routes.

Map 3 corresponds to phase 2B of the La Celle forest succession: only one route from Central Europe is identified, which relates to species with modern distributions still well represented in the North but which extended further south. New incoming species are recorded at all sites of the studied areas.

Maps 4 and 5 include species from phase 2C of the La Celle forest succession: as during phase 2A, two routes from Western and Central Europe are functional. Nevertheless, the species involved were less tolerant and their modern distributions hardly reach the northernmost parts of Europe. In both cases the incoming species failed to colonize the most extreme geographical limits of the studied area during MIS 11 stage, namely Britain for central European species, and Germany for western species.

Map 6 shows species characterizing phases 3D and 3E of the La Celle forest succession: at the maximum development of deciduous forest, immigrant species have the southernmost modern distributions with none present in Scandinavia today. Except *Semilimax semilimax* which is an Alpine and Central European species, all the incoming snails have Mediterranean or South-East European current ranges (Kerney and Cameron, 1979; Welter-Schultès, 2012). Their occurrence suggests a colonization corridor from Mediterranean refugia. Those species are present throughout the three studied areas although not at all the studied sites.

Much evidence shows that during the last glacial period most temperate species retreated to the Mediterranean area but some also survived in northerly micro-refugia (Willis and van Andel, 2004; Tzedakis et al., 2013; Schmitt and Varga, 2012). As terrestrial molluscs are dependent on vegetation, the location of their refugia are likely to be similar especially for ecologically demanding species living in shaded habitats generated by forest. Forest land snail habitats have also been identified during the Last Glacial Maximum in the Western Carpathians (Ložek, 2006; Juříčková et al., 2014) and Hungary (Willis et al., 2000). The populations that inhabit these northern refugia played an important role in recolonization and strongly influenced the distribution of strictly forest species throughout Europe. Indeed, a clear east-west gradient has been identified with more diverse forest species occurring in the east, in contrast to impoverished assemblages from the early Holocene in the west (Horsák et al., 2019). However, more diverse forest assemblages occurred in north-west Europe during several Middle Pleistocene interglacials and the Eemian (Mania et al., 2001; Preece et al., 2007; Antoine et al., 2006; Limondin-Lozouet et al., 2006). Compared to Holocene assemblages, these interglacial molluscan communities were enriched with a number of closed forest species mostly originating from Central Europe (Limondin-Lozouet and Preece, 2014). Among these interglacial malacofaunas, those of MIS 11 are unquestionably the most diverse with almost twice as many species as occurred during MIS 5e and MIS 1 (Limondin-Lozouet and Preece, 2014). The order of arrival of shade-loving species during MIS 11 in North-West Europe showed that Atlantic and Eastern refugia provided primary source populations for recolonization throughout the period of forest expansion (Fig. 9, Table 3). Their order of appearance was determined both by their ecological tolerance and by the distance from their refugial areas. The earliest communities of woodland snails, before the arrival of mixed oak forest, consisted of species with less shade-demanding requirements with broader geographical ranges and closer refugia (Fig. 9: zones 2-A and 2-B). During the development of deciduous forest, new arrivals appear to have originated from the same source areas, but they were more ecologically demanding and did not spread so extensively into the studied region. Lastly, southernmost species including some strictly Mediterranean taxa reached the area only during the deciduous forest maximum, coincident with the climatic optimum.

The island status of Britain raises the question of how the *Lyrodiscus* fauna reached this region during MIS 11. Indeed increasing evidence points to more limited sea level rise, peaking late in the interglacial, suggesting the existence of land bridges between Britain and the continent for longer than in any other interglacial (Candy et al., 2014). The present study lends supports for this interpretation as most of the forest snails from British tufas of MIS 11 age appear to belong to the deciduous forest expansion phase at La Celle (Biozone 2). The additional species known from Hitchin and Beeches Pit, mostly have modern Atlantic ranges, implying that they reached Britain during the phase of forest expansion (Fig. 10: Map 4 phase 2C). Conversely the Mediterranean taxa that characterize the optimum phase (Biozone 3) are poorly represented at British sites, suggesting that by then Britain may have become an island again. However, their rarity/absence might also result from the more oceanic climate of these western sites that would have prevented the northward spread of species with greater sensitivity to enhanced seasonality.

As regards the present ranges of these late immigrant species, the most complete area of overlap appears to be the Alps (Fig. 10:map 6). Their occurrence in north-western Europe during MIS 11 indicates a northward shift of this biodiversity hotspot for terrestrial molluscs. The dense humid forest hosting these highly diverse malacofaunas suggests a difference in climatic conditions when compared with the Holocene. Rousseau (2003; see also Rousseau et al. 1992) thought that the *Lyrodiscus* biome indicated a warmer and wetter climate. This view is reinforced by occurrence of several southern thermophiles including reptiles (*Zamenis longissimus*, *Emys orbicularis*) in Britain (Preece et al., 2007; Holman, 1998), Mediterranean plants (*Ficus carica*, *Celtis australis*, *Buxus sempervirens*) and thermophilous mammals (*Macaca*

*sylvanus*, *Hippopotamus incognitus*) in Northern France (Rousseau et al., 1992; Limondin-Lozouet et al., 2006). Nevertheless, Preece et al. (2007) argued that these observations are relevant only at the local scale and cannot necessarily be taken to infer higher temperatures because this is not apparent reconstructions derived from pollen or isotopic records. Recent palynological studies from marine cores taken off the Iberian margin show that true Mediterranean species were present in MIS 11, MIS 7, MIS 5e and MIS 1, occurring in similar proportions that do not allow the warmest of these last five climatic cycles to be identified (Desprat et al., 2007). Direct comparison of molluscan and geochemical records during MIS 11 is only possible for the La Celle sequence, which points to the consistency of both indicators (Dabkowski et al., 2011, Dabkowski et al., 2012). Similar studies undertaken on Holocene tufas demonstrate that the temperature ranges were close during both interglacials, but the climatic optimum was warmer during MIS 11 (Dabkowski, 2011). Humidity values were also higher during MIS 11 especially during the optimum and the final humid phase at the top of the sequence, consistent with previous suggestions that MIS 11 was generally wetter than MIS 1 (Droxler et al., 2003; Candy et al., 2014). More direct climatic comparisons are needed but given that snails are poor dispersers and that they are completely dependent on vegetation (Simonová et al., 2016), the northward extension of most thermophilous snails during MIS 11 might be more than a local signal.

## 5. Conclusions

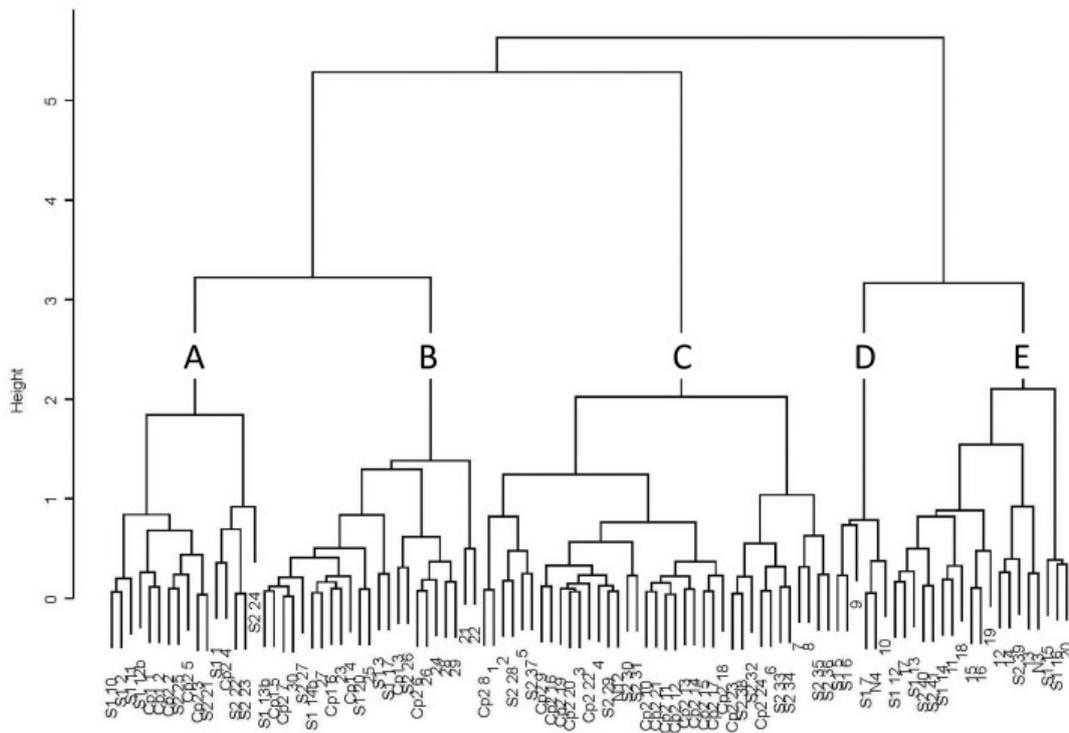
The so-called « *Lyrodiscus* fauna » has been defined as a biochronological feature of tufas of MIS 11 age from North-west Europe. The La Celle sequence yields a particularly long malacological record, in which several forest phases have been identified. It therefore provides a unique opportunity to understand the spread and development of the humid forest biotope hosting the *Lyrodiscus* fauna. La Celle is the longest and only tufa deposit to yield a detailed record of forest expansion during MIS 11. It can therefore be used to build a regional model into which other less complete sequences can be placed shedding light on palaeoenvironment dynamics, biostratigraphy, palaeogeography and palaeobiodiversity.

Successive occurrences of forest snails appear to reflect increasing temperatures. Earlier arrivals of shade-loving species indicate the spread of pioneer forest. The replacement of *Discus ruderatus* by *Discus rotundatus* appears to reflect the expansion of deciduous forest. Maximum of malacological diversity coincided with the temperature and humidity optima. The disappearance of most forest snails can be linked to a decrease in temperatures.

Detailed comparison of the land snail assemblages from tufa deposits in northern France and South-east England suggests that almost all the limited successions correspond to the maximum development of the humid forest biotope during MIS 11c. The assemblages from the Saint-Acheul and Arrest tufas appear to relate to the development of deciduous forest immediately preceding the optimum. The assemblages from the tufas at Beeches Pit, Hitchin, St Pierre-lès-Elbeuf and the lower part of Vernon yielded well-developed forest faunas similar to those of the richest assemblages from the climatic optimum at La Celle. The assemblage from the upper levels at Vernon resemble the latest assemblages from La Celle characterized by greatly reduced frequencies of woodland snails and the appearance of those of open-ground.

The order of occurrence of forest snails suggests that Atlantic and central European refugia were the source populations for the recolonization of north-western Europe. Southermost taxa including some strict Mediterranean species reach the area only during the climatic optimum. Many species present during MIS 11 no longer live in the study area. Their occurrence demonstrates a northward shift of the malacological biodiversity hotspot during MIS 11.

The following are the supplementary data related to this article.



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Fig. S1. Hierarchical ascendant classification of the La Celle malacological data set.

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Tables S1 to S5. Occurrence of Mollusca in the La Celle profiles S2, Cp2, Cp1, S5, S1.

## Declaration of Competing Interest

None.

## Acknowledgements

We are indebted to Dr. Richard Preece of the University of Cambridge for his comments and the English editing that greatly improved the manuscript. We are grateful to Clément Vermoux (CNRS- LGP) for help in designing maps of Fig. 10. We thank three anonymous reviewers for useful comments on the manuscript. This paper is a contribution to ANR project NEANDROOTS.

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