



REVIEW ARTICLE

Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe

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ABSTRACT

The land snail assemblages in NW Europe exhibit marked gradients in diversity related to both latitude and longitude. These gradients, in turn, are linked to regional differences in temperature and moisture, although other non-climatic factors may be involved. Such diversity patterns have been described for the modern land snail faunas of NW Europe, especially those that inhabit forest. Here we provide an historical perspective on the development and composition of comparable land snail assemblages from various interglacials from the Middle and Late Pleistocene, and from the Holocene. We review the land snail assemblages from tufa sequences, which provide the best faunal records for each of the temperate periods. Data from 32 Quaternary sites in 7 NW European countries are considered. Assemblages from ‘forest optima’ of Pleistocene interglacial periods are richer in species compared with those from the Holocene. Correspondence analysis (CA) of data from 25 Quaternary sites in the regions where both Pleistocene and Holocene sites occur (i.e. southern England, northern France and Germany) resulted in a geographical separation of the assemblages into a western and eastern group. CA on each geographical group resulted in chronological divisions separating Pleistocene sites from the Holocene sequences. This separation results from the occurrence of numerous Central and Eastern European species in the Pleistocene faunas, whereas Holocene assemblages are characterized by species with mostly Western and Northern European modern ranges. This difference appears to reflect climatic influences, rather than resulting from anthropogenic effects. CA of 19 Holocene tufas produced geographical clusters clearly related to their position on a west-east gradient, presumably linked to some effect of ‘continentality’. During the mid Holocene, the diversity of forest snails from tufas in southern England exceeded the totals from the richest calcareous woodland sites in the region today. Further work is needed to establish whether this pattern holds for other regions of NW Europe.

INTRODUCTION

At a broad scale, the geographical distributions of land snails in Europe are now reasonably well known (e.g. Kerney, Cameron & Jungbluth, 1983; Welter-Schultes, 2012). There is an increase in species richness from north to south, and to a lesser extent from west to east. These distributional patterns are determined in part by the oceanicity and continentality gradients of the climate, but also result from a variety of other causes, both ecological and historical. Southern Europe hosts the greatest number of land snail species, including many endemics with very restricted ranges. In a number of locations the restricted ranges of a series of endemics overlap to form biodiversity ‘hotspots’, which are of major interest and concern to biologists and conservation agencies alike

(Cuttelod, Seddon & Neubert, 2011). Such endemics are likely to have arisen in these localized areas where they have survived the climatic vicissitudes of the Pleistocene cold stages (Holyoak, 1989).

Not only is the species richness higher in southern populations, but the genetic diversity is also likely to be higher, especially in areas that served as refugia for thermophilous species during the coldest parts of the Pleistocene (cf. Hewitt, 1996, 2004). In general, the species richness (and genetic diversity) of northern populations is invariably less than in those from southern Europe, but this pattern is not maintained at smaller spatial scales. Pokryszko & Cameron (2005) cite a number of examples of sites in northern Europe where the number of land snail species in areas of 1 km<sup>2</sup> or less exceeds that at many southern European sites and rivals that observed in some subtropical areas.

During the cold stages of the Pleistocene, much of NW Europe was covered by ice sheets and the periglacial regions beyond the ice limits would have been rendered inhospitable for most species of thermophilous snail. Biogeographical patterns, such as those just described, therefore largely represent the results of postglacial immigration from refugial areas to the south (e.g. [Taberlet et al., 1998](#); [Hewitt, 1999](#)). The extent of ice cover and the severity of the climate during different cold stages varied and had an important influence on the biotic history of the ensuing interglacials. During extremely severe climates, certain thermophilous species are likely to have been displaced into more distant refugia, resulting in their delayed appearances during the ensuing interglacials.

Sea level fell by about 130 m during cold stages, converting much of the shallow continental shelf into dry land. These major palaeogeographical changes afforded new opportunities for species colonizing from the south. For example, species would have had unimpeded access to Britain, which became a peninsula of NW Europe during each cold stage, only becoming an island again during the early part of the ensuing interglacial ([Preece, 1995](#)). The situation of Ireland regarding island status is more problematic.

Interglacials differ in the intensity of their warmth, in their overall climatic structure and in their duration, which in turn influence their biological composition. The biotic history of each interglacial therefore partly reflects the legacy of the climatic character of the previous cold stage, as well as the conditions that existed during the interglacial itself. Each interglacial is therefore likely to have its own individual biotic signature, reflecting the interplay of all these factors. Human influences on the environment were negligible before the Holocene and can be ignored.

The purpose of this paper is to compare the richness and composition of land snail assemblages during successive Pleistocene interglacials during the last ~450 kyr and to compare this with the situation that occurred during the Holocene and at the present day. Land snails are a suitable group for evaluating the development of diversity during the Quaternary because they occur commonly as fossils and even small fragments of shell can usually be identified to species level. Fossil assemblages can be recovered from a range of depositional environments, which will each furnish a slightly different faunal composition, depending on taphonomy and ecology. When making comparisons, it is therefore important to reduce any effects resulting from such causes and to focus on the assemblages from one type of depositional context. For reasons discussed below, we here consider only land snail assemblages from calcareous tufas in our review of Quaternary data. This study focuses specifically on the richness and composition of land snail assemblages from forest environments, since these are the most informative and show the strongest regional differentiation. These comparisons provide a temporal perspective on the development of diversity through the Quaternary and on the modern biogeographical patterns that exist today in NW Europe.

## MATERIAL AND METHODS

### *The importance of tufas*

If faunal comparisons are to be biologically meaningful, it is important to attempt to standardize the choice of sites included in the analyses. For this reason, we focus exclusively on the molluscan records from calcareous tufas, since these deposits have enormous advantages over other types of sedimentary record ([Preece, 1991](#)). First, since tufas are composed of calcium carbonate precipitated in the vicinity of springs and in alluvial situations, they usually contain the richest communities of land snails from any region. Second, the calcareous nature of the

sediment greatly improves the preservation potential of fossil shells and it is even possible to recover the feebly calcified shells of species such as *Zenobiella subrufescens*. The excellent preservation of shells in tufas also minimizes the problems of identification, allowing even tiny fragments and apices to be determined with confidence (e.g. [Preece, 1981](#)). Third, tufas usually accumulated in low-energy environments and often provide more-or-less continuous records covering several millennia. Moreover, within fluvial terrace systems in NW Europe they are invariably the only deposits that preserve registration of peak interglacial conditions ([Antoine & Limondin-Lozouet, 2004](#)). Fourth, tufas usually contain virtually autochthonous communities of land snails that lived and died where they are now found. It is therefore possible to recover biologically meaningful assemblages from such low-energy depositional environments, in contrast to those recovered from fluvial contexts, which often represent species derived from a wide spectrum of habitats indiscriminately mixed together.

As well as yielding rich assemblages of molluscs, tufas also contain records from a variety of other fossil groups with which the molluscan sequences can be compared. In waterlogged conditions organic fossils may also be preserved, including pollen, so that in such situations it may be possible to link malacological and vegetational records (e.g. [Kerney, Preece & Turner, 1980](#); [Preece & Day, 1994](#); [Preece & Bridgland, 1999](#); [Limondin-Lozouet, Gauthier & Preece, 2005](#)). Furthermore it is possible to obtain records of climatic history from analyses of stable isotopes (and trace elements) from the tufa itself, which in turn can be directly related to the malacological sequence that it contains ([Garnett et al., 2004](#); [Andrews, 2006](#); [Dabkowski et al., 2011, 2012](#)). Finally, several methods of dating can be used either on material recovered from the tufa or on the tufa matrix itself in order to build good chronologies for the molluscan sequences.

Tufas form in both spring environments and in alluvial contexts, providing reliable sources of clean fresh water that were highly attractive habitats for early humans. Consequently, many tufas have yielded archaeological artefacts, especially Mesolithic flint flakes in Holocene sequences (e.g. [Evans, 1972](#); [Preece, 1980](#); [Preece et al., 1986b](#)), whereas some Pleistocene interglacial tufas have yielded Palaeolithic archaeology (e.g. [Antoine et al., 2006](#); [Limondin-Lozouet et al., 2010](#); [Locht, Goval & Antoine, 2010](#)), including the remains of hominins themselves, as at Bilzingsleben and Weimar-Ehringsdorf in Germany ([Vlček, 1993](#); [Mania, 1995a](#); [Street, Terberger & Orschiedt, 2006](#)).

### *Sites*

Details of the 32 tufa sites included in this study are given in Table 1 and their locations plotted in Figure 1. The records for three pairs of neighbouring sites, two pairs in Ireland (Graffy and Catronmacmanus in County Mayo, Millpark and Gloster in County Offaly) and one pair in England (Courteenhall and Weston Favell in Northamptonshire) have been included as three composite (rather than six individual) entries for each respective county. Tufas belonging to two different interglacial stages [marine isotope stage (MIS) 11 and MIS 9] occur at Bilzingsleben (II and III respectively) and the assemblages from these have obviously been treated separately. In order to reduce any effects resulting from the varied experience of different workers, we have selected fossil sites where we have either performed the faunal analyses ourselves or have used data from those sites where we have overseen the work undertaken. The exceptions are the sites in eastern Germany, but these have been analysed to a high standard and we consider the data of comparable quality to the other sites considered here (see [Meyrick & Schreve, 2002](#), for a discussion about the ages of critical Pleistocene sites in Thuringia).

The tufas are located in seven countries and cover a latitudinal range of 45–58°N and a longitudinal range of 8°W–14°E

**Table 1.** The Quaternary tufas reviewed here giving details of their location, geographical coordinates, age, species composition and the primary references to work undertaken on them.

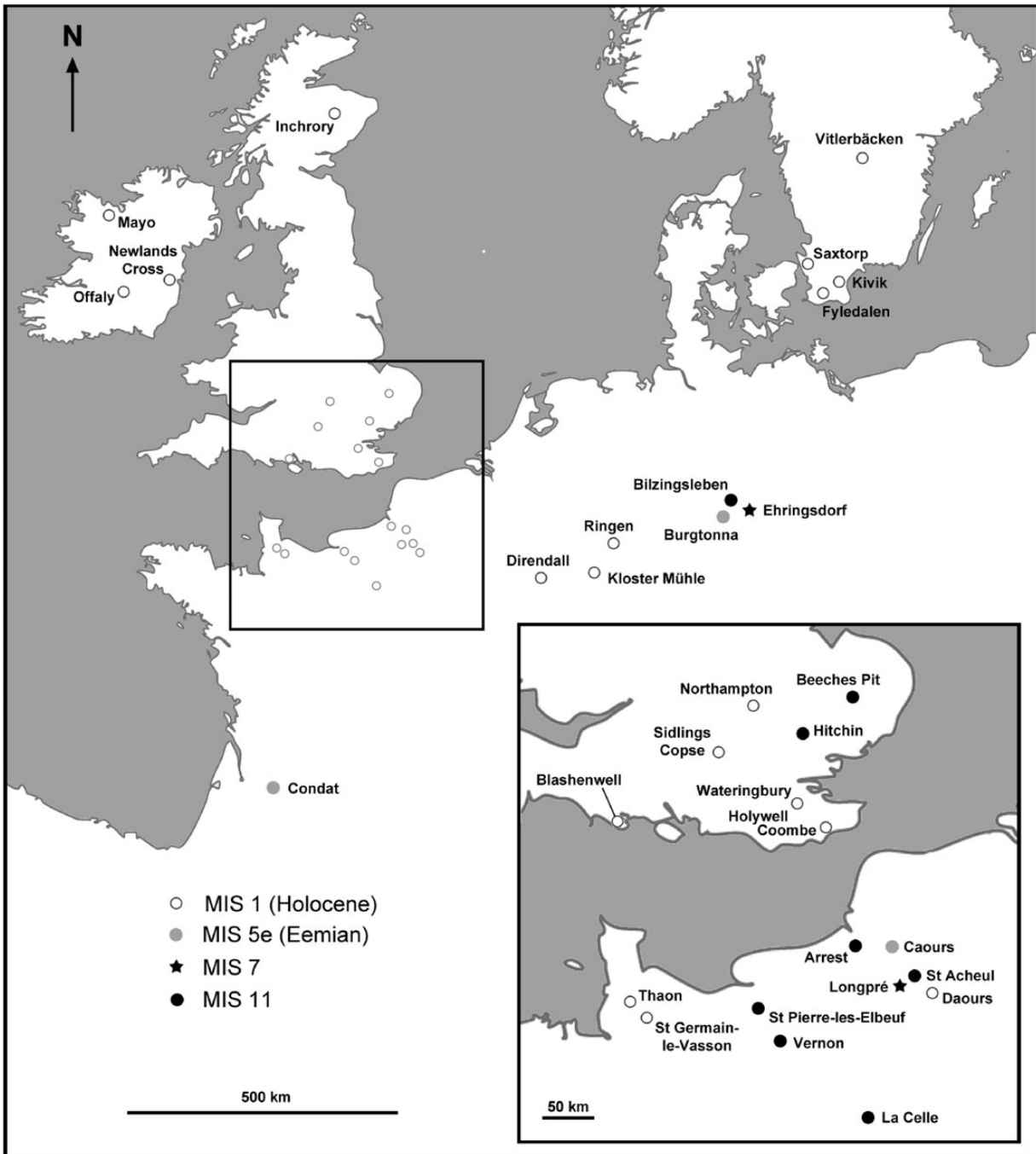
Location	Country	Latitude	Longitude	Age	Land snail species (total)	Forest species	References
Mayo (Graffy & Cartronmacmanus)	Ireland	54°00'N	08°58'W	MIS 1	35	15	Speller (2006)
Offaly (Millpark & Gloster)	Ireland	52°58'N	07°49'W	MIS 1	39	17	Preece & Robinson (1982)
Newlands Cross, Co Dublin	Ireland	53°18'N	06°23'W	MIS 1	35	15	Preece <i>et al.</i> (1986a), Speller (2006)
Inchrory, near Tomintoul, Banffshire	Scotland	57°09'N	03°21'W	MIS 1	23	10	Preece, Bennett & Robinson (1984)
Blashenwell, near Corfe, Dorset	England	50°37'N	02°04'W	MIS 1	38	16	Preece (1980)
Sidlings Copse, near Oxford	England	51°46'N	01°11'W	MIS 1	37	15	Preece & Day (1994)
Northampton (Courteenhall & Weston Favell)	England	52°0'N	00°52'W	MIS 1	50	18	Meyrick & Preece (2001)
Wateringbury, near Maidstone, Kent	England	51°15'N	00°25'E	MIS 1	47	20	Kerney <i>et al.</i> (1980), Garnett <i>et al.</i> (2004)
Holywell Coombe, Folkestone, Kent	England	51°05'N	01°10'E	MIS 1	55	17	Kerney <i>et al.</i> (1980), Preece (1998), Preece & Bridgland (1999)
Hitchin, Hertfordshire	England	51°57'N	00°17'W	MIS 11	36	23	Kerney (1959), Preece <i>et al.</i> (2007)
Beeches Pit, West Stow, Suffolk	England	52°18'N	00°40'E	MIS 11	43	26	Kerney (1976), Preece <i>et al.</i> (2007)
Thaon, Calvados	France	49°15'N	00°27'W	MIS 1	35	16	Lespez <i>et al.</i> (2008)
St Germain-le-Vasson, Calvados	France	48°59'N	00°18'W	MIS 1	42	21	Limondin-Lozouet & Preece (2004), Limondin-Lozouet <i>et al.</i> (2005)
Daours, Somme	France	49°53'N	02°27'E	MIS 1	40	18	Limondin-Lozouet, Preece & Antoine (2013)
St Pierre-les-Elbeuf, Seine maritime	France	49°16'N	01°02'E	MIS 11	45	27	Rousseau <i>et al.</i> (1992), Cliquet <i>et al.</i> (2009)
St Acheul, Somme	France	50°11'N	02°09'E	MIS 11	43	23	Antoine & Limondin-Lozouet (2004), Limondin-Lozouet & Antoine (2006)
Vernon, Eure	France	49°05'N	01°29'E	MIS 11	56	33	Rousseau <i>et al.</i> (1992)
Arrest, Somme	France	50°07'N	01°36'E	MIS 11	35	25	Rousseau <i>et al.</i> (1992)
La Celle-sur-Seine, Seine et Marne	France	48°23'N	02°50'E	MIS 11	70	33	Limondin-Lozouet <i>et al.</i> (2006, 2010), Dabkowski <i>et al.</i> (2011, 2012)
Longpré-lès-Corps Saints, Somme	France	50°00'N	01°59'E	MIS 7	38	15	Bourdier <i>et al.</i> (1974), Limondin-Lozouet (unpubl.)
Caours, Somme	France	50°07'N	01°52'E	MIS 5e	53	26	Antoine <i>et al.</i> (2006), Dabkowski <i>et al.</i> (2011)
Condat-sur-Vézère, Dordogne	France	45°07'N	01°3'E	MIS 5	43	20	Preece <i>et al.</i> (1986b), Limondin-Lozouet <i>et al.</i> (2012)
Direndall, near Kopstal	Luxembourg*	49°41'N	06°06'E	MIS 1	42	21	Meyrick (1998, 2000)
Ringgen, Rheinland-Pfalz	Germany*	50°34'N	07°06'E	MIS 1	51	22	Meyrick (1998, 2001)
Kloster Mühle, Welschbillig, Rheinland-Pfalz	Germany*	49°51'N	06°35'E	MIS 1	42	18	Meyrick (1998, 2001, 2003)
Burgtonna, Thuringia	Germany	51°03'N	10°43'E	MIS 5e	75	35	Mania (1978)
Ehringsdorf, Weimar, Thuringia	Germany	50°57'N	11°20'E	MIS 7	66	28	Mania (1993), Mania & Mai (2001)
Bilzingsleben II, northern Thuringia	Germany	51°16'N	11°04'E	MIS 11	72	38	Mania & Mai (2001)
Bilzingsleben III, northern Thuringia	Germany	51°16'N	11°04'E	MIS 9	57	28	Mania & Mai (2001)
Fyledalen, south-central Skåne	Sweden	55°34'N	14°51'E	MIS 1	25	10	Gedda (2001)
Saxtorp, western Skåne	Sweden	55°50'N	12°58'E	MIS 1	39	16	Gedda (2001)
Kivik, eastern Skåne	Sweden	55°41'N	14°12'E	MIS 1	40	16	Gedda (2001)
Vittlerbacken, Östergötland	Sweden	58°21'N	14°39'E	MIS 1	34	18	Meyrick (1998)

MIS, marine isotope stage; MIS 1, Holocene; asterisk, Rheinland sites. Forest species are as defined by Ložek (1964) and Puisségur (1976).

(Table 1). Using the LR04 chronology of Lisiecki & Raymo (2005) for MIS boundaries, the tufa sequences reviewed formed during the following periods. Nineteen are Holocene (MIS 1 that commenced 14 ka ago) in age, two belong to the last interglacial (Eemian, MIS 5e, 130–116 ka, peak at 123 ka), one site (Bilzingsleben III) has been attributed to MIS 9 (337–300 ka), and eight formed during MIS 11 (424–374 ka). We include the data from one site (Longpré-lès-Corps Saints) belonging to MIS

7 (243–191 ka), although the record does not seem to represent peak interglacial conditions (Bourdier *et al.*, 1974). The same applies to the record from the Condat tufa, the most southerly site considered, but the tufa here nevertheless formed during MIS 5 (Limondin-Lozouet *et al.*, 2012).

The geographical coverage of tufa sites with good molluscan records is best for the Holocene. Indeed, data from further Holocene tufa sites could have been included from southern



**Figure 1.** Location map of tufa sequences mentioned in the text (see [Table 1](#) for details of each site).

England but the records from the five sites chosen are thought to be good representatives from this region. Records from elsewhere are more patchy and we have included the only available data from Holocene tufa sites in Ireland, Scotland, France and Luxembourg. Further data exist for a few other tufa sites in southern Sweden ([Gedda, 2001](#)), but these have yielded wetland assemblages lacking forest species and have consequently been excluded. In NW Europe, good interglacial molluscan sequences from tufas are known only from Germany and France, where records from MIS 11, MIS 9, MIS 7 and MIS 5e are available. Land snail assemblages from two tufas of MIS 11 age are also known from southern England, but though the records span only relatively brief parts of that interglacial they include the ‘forest optimum’.

#### *Land snails included in the analyses*

We provide details of the total number of species of land snail recorded at each site ([Table 1](#)), but focus specifically on those that inhabit forest habitats. As mentioned above, forest snails are the most informative and regionally differentiated, and data on forest communities from modern sites exist with which comparisons can be made.

‘Woodland snails’ require definition since the extent to which certain species are shade-demanding can depend on their geographical location, several species showing more exacting requirements towards the margins of their range (e.g. [Kerney, 1968](#)). Species regarded as typical of closed forest in one region might



therefore occur in less forested habitats in other regions. Since this study is NW European in scope, we essentially use the ecological classifications of Ložek (1964) and Puisségur (1976) to define the species assigned to forest biotopes (see Supplementary Material). The ‘forest species’ are those included within ecological groups W and 1, 2 and 3 of their schemes. Some species with more southern modern distributions have been added following more recent work on faunas from SW France (Limondin, 1990).

Slugs are excluded from the analyses, since fossil slug remains cannot be reliably assigned to species. The burrowing subterranean species *Cecilioides acicula* is also excluded because of uncertainties about its status.

As regards the modern ranges of particular species and their attribution to particular biogeographical regions (e.g. ‘Central European’), we follow Kerney *et al.* (1983) and Welter-Schultes (2012).

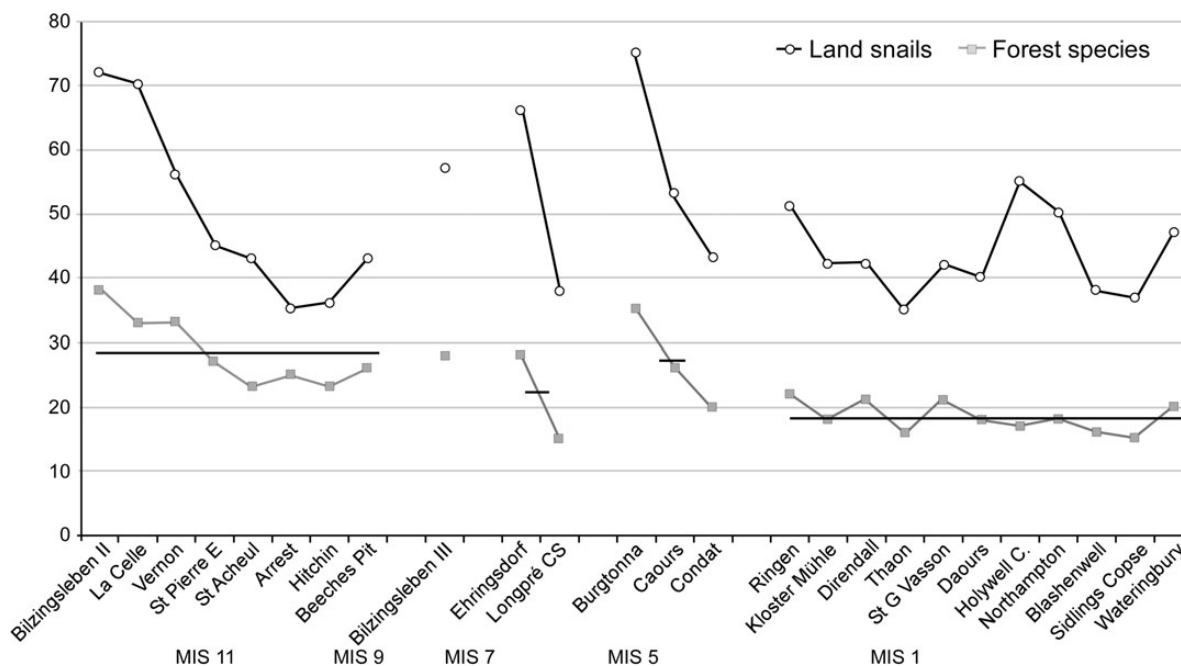
The broad-scale distribution of land snails in NW Europe is reasonably well known, but there is surprisingly little quantitative information on forest assemblages from individual sites. Cameron & Pokryszko (2005) have developed standard sampling protocols, which have been undertaken in southern England (Cameron, Pokryszko & Long, 2006) and elsewhere (Pokryszko & Cameron, 2005) and these have provided much of the data relating to modern faunas from different regions. In order to standardize the comparisons between modern woodland faunas in southern England with Holocene assemblages from the same region, we only include records of woodland snails from the ‘forest optimum’. The ‘forest optimum’ is defined here as the stratigraphical levels of the tufa yielding the maximum frequency of forest snails. For the Holocene this is usually the period between ~9 and 6 ka before present (BP), which pre-dates the major forest clearance episodes that occurred during the Neolithic and Bronze Age.

## COMPARISONS

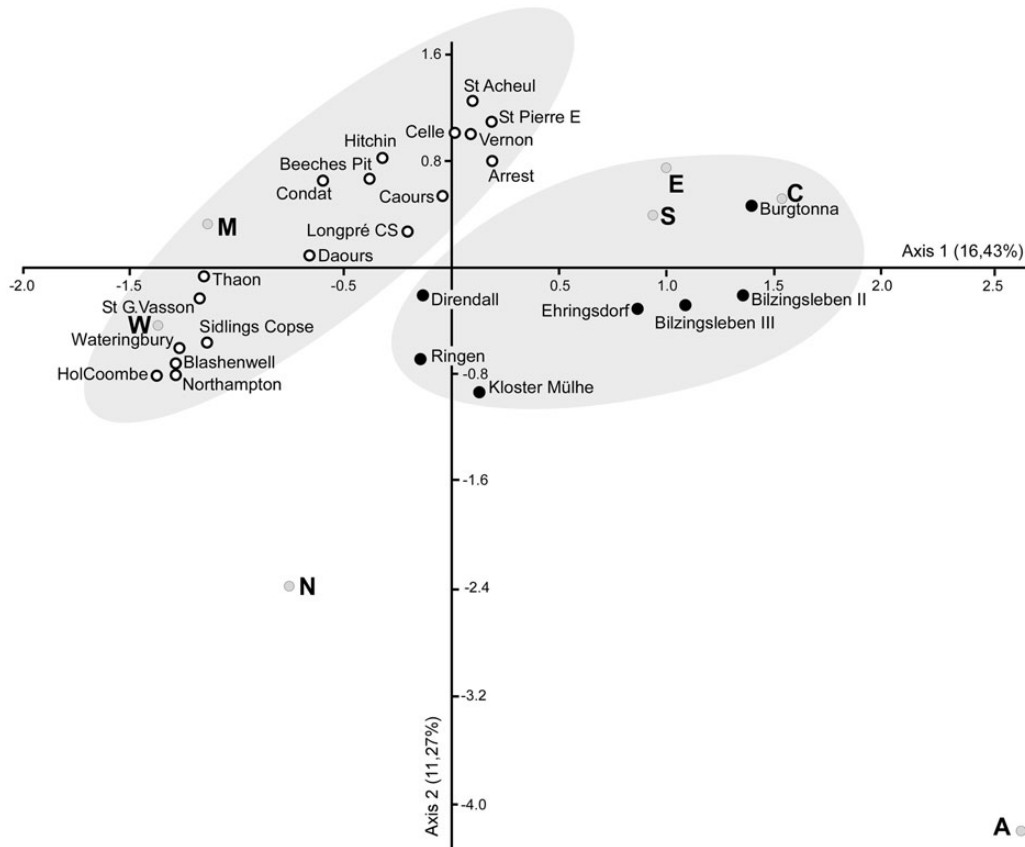
The first question to address is whether there are any differences in species richness or composition between the Pleistocene interglacial forest assemblages and those that occurred during the

‘forest optimum’ of the Holocene. Figure 2 plots the overall richness of land snails and the number of forest species recovered from those regions where both Pleistocene interglacial and Holocene records exist, namely southern England, France and Germany. Data from 25 tufas sequences ranging in age from MIS 11 to the mid Holocene are included in this first comparison. Various points emerge. First, the total number of species recovered from each site is rather variable and presumably dependent on the heterogeneity of microhabitats represented and on the duration of the fossil record concerned. There is slightly more consistency in the number of forest species present, although this too is quite variable. The clear point that emerges is the fact that Pleistocene interglacial species richness of forest snails exceeds that known from Holocene sites across a relatively wide geographical area. This pattern would become even clearer were Longpré and Condat to be excluded, because neither site appears to represent peak interglacial conditions. Better data relating to MIS 9 and MIS 7 are needed, but it is clear from the plots of forest species that there is a loss of diversity from Middle Pleistocene interglacials to the Holocene. The mean number of forest snails at each site is consistently above 25 during Pleistocene temperate periods, whereas it falls below 20 during the Holocene (Fig. 2). There is a suggestion that interglacial richness attained maximum values during MIS 11, but more data from later interglacials would be needed to establish this.

What are the missing species and why are they not present during the Holocene? To address these questions multivariate analyses were undertaken on the Quaternary dataset. This consists of the same 25 sites considered in Figure 2 and the 62 species of forest snail recovered from them, together with their modern European geographical ranges. The ranges fall into seven categories (Kerney *et al.*, 1983; Welter-Schultes, 2012): Northern, Western, Central, Eastern and Southern European, Mediterranean and Alpine. A correspondence analysis (CA) on the whole dataset produced a geographical division of the sites into an ‘Atlantic province,’ grouping sites from France and Britain, and a ‘Continental province’ that includes the sites from Luxembourg and Germany (Fig. 3). This separation results from



**Figure 2.** Plots of total number of land snails and number of forest species recorded at Quaternary sites in Germany, France and southern England (see Fig. 1 for locations). Sites are arranged in order of age with the oldest (MIS 11) on the left of the figure and the youngest Holocene (MIS 1) sites on the right. Gaps are left between each interglacial series. The horizontal black lines indicate the mean totals of forest snails.



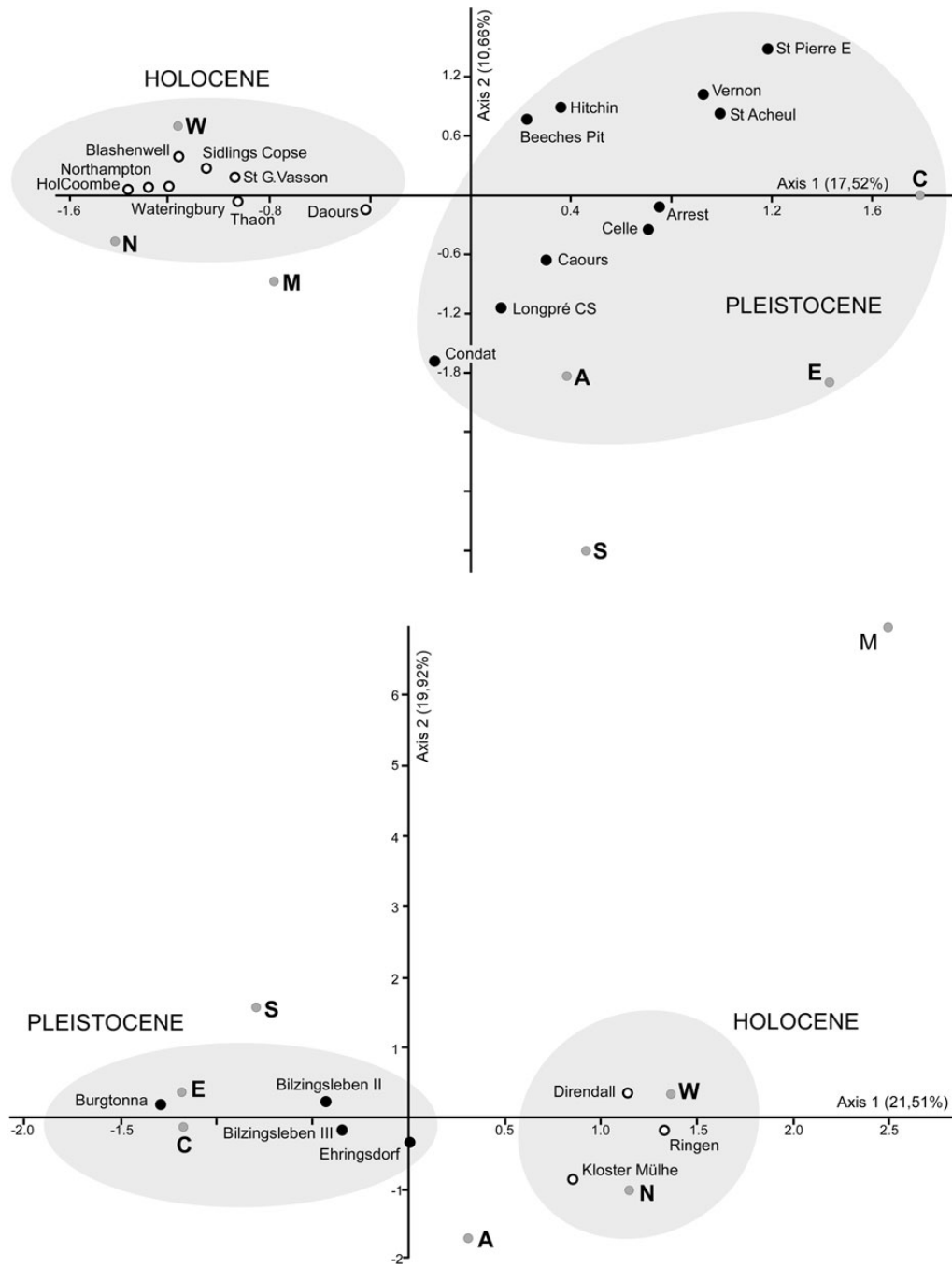
**Figure 3.** A correspondence analysis undertaken on the complete dataset of sites reviewed in Figure 2. The sites fall into a western and eastern group. Black circles indicate Pleistocene sites, white circles Holocene sites, and grey circles the modern geographical ranges of species [Northern (N), Western (W), Central (C), Eastern (E) and Southern European (S), Mediterranean (M) and Alpine (A)].

the exclusive occurrence of certain species within each province. The ‘Atlantic province’ is characterized by species with Western European and Mediterranean modern ranges (such as *Spermodaea lamellata*, *Leiostylia anglica*, *Nematlanta pauli*, *Ashfordia granulata*, *Zonitoides excavatus*, *Pomatias elegans* and *Lauria cylindracea*), whereas the ‘Continental province’ contains species with Eastern, Central and Southern European species (such as *Macrogastra lineolata*, *Discus perspectivus*, *Nesovitreia petronella*, *Isognomostoma isognomostomos*, *Drobacia banatica*). A second CA was then performed on each of these geographical provinces to see if the sites could be separated by age. The results are similar for both provinces (Fig. 4) and show a clear separation of Pleistocene faunas associated with species that now have Central and Eastern European ranges and the faunas from the Holocene containing a greater preponderance of species with Western and Northern European modern ranges. These comparisons demonstrate that the Pleistocene faunas include Eastern and Central European components that are absent from the Holocene.

The next point to address is how these different diversity patterns arose during different interglacials and whether they differ from the successions observed in the Holocene. The source publications (Table 1) contain quantitative data of land snail successions through the various tufa sequences and should be consulted for full details. In Figure 5 the stratigraphical occurrences of critical forest species have been simplified in order to show the pattern of colonization during MIS 11, MIS 5e and the Holocene (MIS 1) for three sites in northern France. The earliest land snail assemblages at each site are represented by wetland species indicating the occurrence of marshland. Forest species do not appear until later. Their appearance is not simultaneous, but shows distinct patterns of colonization. At La Celle

(MIS 11) and Caours (MIS 5e) species with Northern and Western modern ranges appear first, then others with Western and Central ranges and finally those with Eastern and Southern European ranges (Fig. 5; Table 2). A similar pattern is seen in the Holocene tufa at St Germain-le-Vasson, but there the sequence does not include the critical elements with Central and Southern modern ranges. For the Pleistocene sequences, it is during this last episode with Central and Southern species that the richest forest snail assemblages occur. These episodes broadly coincide with the climatic optima of the interglacials (Fig. 5), after which forest habitats decline and no further waves of forest species appear (Antoine *et al.*, 2006; Limondin-Lozouet *et al.*, 2006). Comparison with earlier interglacial records suggests that during the Holocene these Central and Southern European elements should have reached Western Europe during the so-called Atlantic period between 8 and 5 ka BP, when the climate was at its optimum. The absence of these exotic elements during the Holocene cannot be attributed to human impact since they should have occurred before the major forest disturbance events that took place from the Neolithic and later periods.

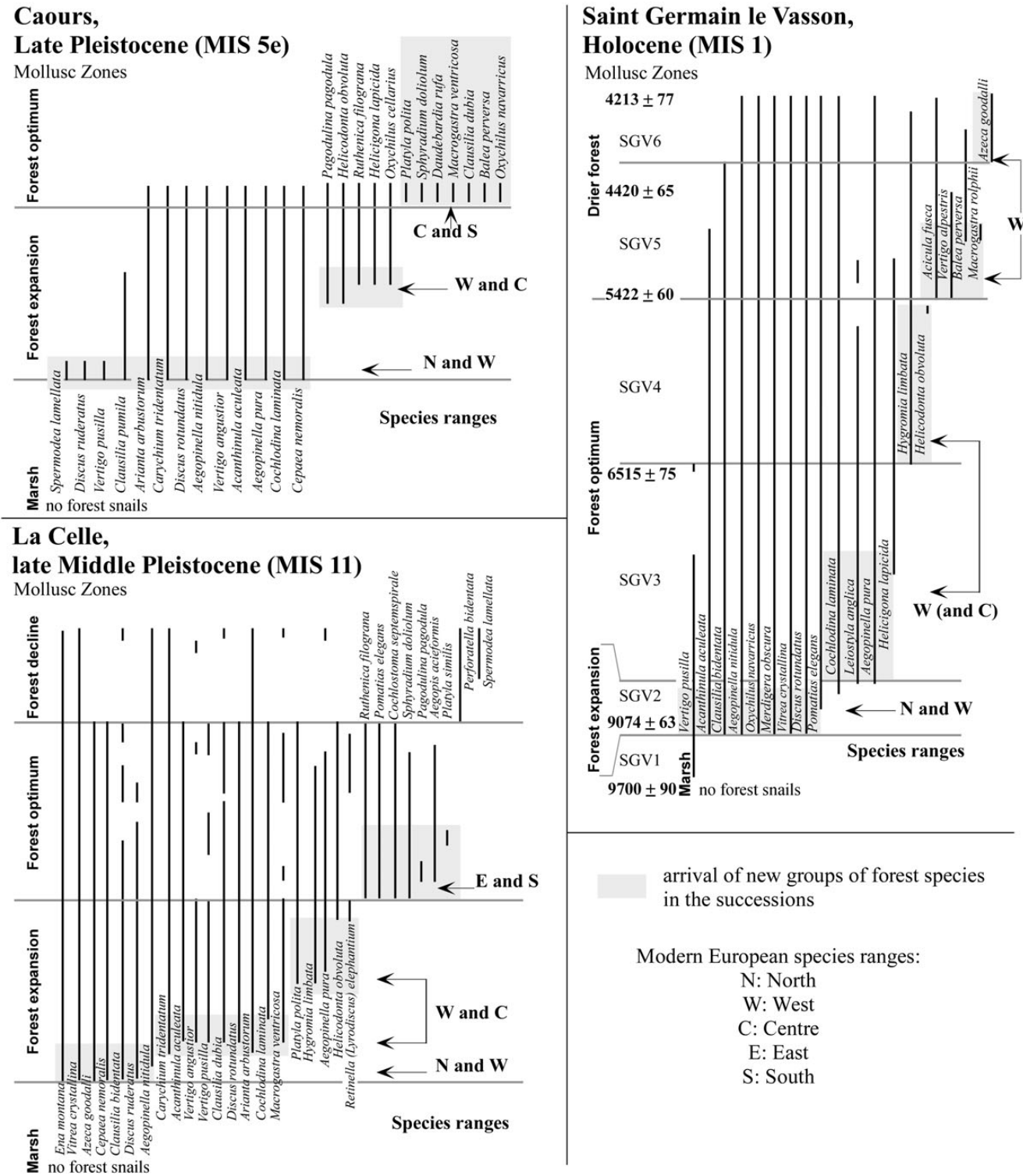
The critical species in each of the biogeographical groups are listed in Table 2, together with their occurrence in different temperate periods (MIS 11, MIS 5e and the Holocene) and in modern Polish forests (Cameron & Pokryszko, 2004; Cameron, Pokryszko & Horsák, 2010). Assemblages dating from MIS 11 have the greatest number and diversity of forest snails that make up a highly distinctive assemblage and forms part of the so-called ‘*Lyrodiscus* biome’ (Rousseau, Puisségur & Lécalle, 1992). This takes its name from the subgenus of one of the important species, *Retinella* (*Lyrodiscus*) *elephantium*, which occurs in



**Figure 4.** A correspondence analysis undertaken on each of the geographical groups identified in Figure 3. In both regions a clear chronological separation is seen between Pleistocene sites associated with Central and Eastern European species and Holocene sites characterized by species with Western and Northern European modern ranges. See details in caption of Figure 3.

this fauna. This species is extinct, but the subgenus *Lyrodiscus* still survives on the Canary Islands, where it is represented by a number of species (Rousseau & Puissegur, 1990; Alonso *et al.*, 2013). Four other extinct land snails, presumably all forest dwellers from the associated species, occur in the *Lyrodiscus* fauna (Table 2). The Pleistocene occurrence of one of these (*Zonitoides sepultus*) was discussed further by Preece & Meijer (2002). Other ‘Atlantic’ elements include *Zenobiella subrufescens* and *Neniatlanta pauli*, which is now confined to woods in the foothills of the French Pyrenees (Welter-Schultes, 2012). These species occurred with many that now live in Central and Eastern Europe

(e.g. *Platyla polita*, *Ruthenica filograna*, *Macrogastra ventricosa* and *Clausilia pumila*), as well as a few that now have Southern European ranges (e.g. *Platyla similis*). The ‘*Lyrodiscus* fauna’ consisted of more than twenty ‘exotic’ species that represented a peculiar biotope of humid forest, which included some Mediterranean trees. It is therefore a nonanalogue assemblage with no modern counterpart. Recent reappraisal of data from MIS 11 tufas indicates that the ‘*Lyrodiscus* assemblage’ is restricted to the western part of Europe, where it occurs at five sites in northern France and two from southern England. The contemporaneous faunas from Germany have yielded *Lyrodiscus* but not the other critical



**Figure 5.** Schematic diagrams showing the progressive appearance of forest species during MIS 11 (La Celle), MIS 5e (Caours) and during the Holocene (MIS 1: St Germain-le-Vasson) in northern France. Note the similarities between the two interglacial sequences and the scarcity of Central and Eastern European species during the Holocene. The dates from St Germain-le-Vasson are uncalibrated radiocarbon years before present.

species that characterize this assemblage (Limondin-Lozouet & Antoine, 2006). The MIS 11 faunas from northern France and southern England are remarkably similar, although some of the French sites contain species (e.g. *Pagodulina pagodula*, *Hygromia limbata* and *Aegopinella bourdieri*) unknown as fossils in southern England (Preece et al., 2007; Table 1).

The record for the last interglacial (Eemian) is based on the sequences from Caours in northern France (Antoine et al., 2006) and Condat in southwestern France (Preece et al., 1986b; Limondin-Lozouet et al., 2012). In contrast to the assemblages from MIS 11, the forest fauna contains fewer species, critical elements of the *Lyrodiscus* fauna are missing (including *Lyrodiscus*



**Table 2.** List of forest snails in Pleistocene (MIS 11 and MIS 5e) and Holocene (MIS 1) tufas from Western Europe (northern France and southern England), together with their modern biogeographical ranges.

Modern ranges	Western European Quaternary tufas		MIS 1 (Holocene)	Present in Modern Polish forests
	MIS 11	MIS 5e (Eemian)		
East & Centre	<i>Discus ruderratus</i>	<i>Discus ruderratus</i>	<i>Discus ruderratus</i>	<i>Discus ruderratus</i>
	<i>Helicodonta obvolvata</i>	<i>Helicodonta obvolvata</i>	<i>Helicodonta obvolvata</i>	<i>Helicodonta obvolvata</i>
	<i>Ena montana</i>		<i>Ena montana</i>	<i>Ena montana</i>
	<i>Platyla polita</i>	<i>Platyla polita</i>		<i>Platyla polita</i>
	<i>Pagodulina pagodula</i>	<i>Pagodulina pagodula</i>		<i>Pagodulina pagodula</i>
	<i>Ruthenica filograna</i>	<i>Ruthenica filograna</i>		<i>Ruthenica filograna</i>
	<i>Macrogastra ventricosa</i>	<i>Macrogastra ventricosa</i>		<i>Macrogastra ventricosa</i>
	<i>Fruticicola fruticum</i>	<i>Fruticicola fruticum</i>		<i>Fruticicola fruticum</i>
		<i>Daudebardia rufa</i>		<i>Daudebardia rufa</i>
	<i>Cochlodina orthostoma</i>			<i>Cochlodina orthostoma</i>
	<i>Macrogastra plicatula</i>			<i>Macrogastra plicatula</i>
	<i>Clausilia dubia</i>			<i>Clausilia dubia</i>
	<i>Clausilia pumila</i>			<i>Clausilia pumila</i>
	<i>Balea biplicata</i>			<i>Balea biplicata</i>
	<i>Perforatella bidentata</i>			<i>Perforatella bidentata</i>
				<i>Monachoides incarnatus</i>
South	<i>Platyla similis</i>			
	<i>Vitrea subrimata</i>			
	<i>Cochlostoma septemspirale</i>	<i>Cochlostoma septemspirale</i>		
	<i>Sphyradium doliolum</i>	<i>Sphyradium doliolum</i>	<i>Sphyradium doliolum</i>	<i>Sphyradium doliolum</i>
Western	<i>Aegopinella nitidula</i>	<i>Aegopinella nitidula</i>	<i>Aegopinella nitidula</i>	<i>Aegopinella nitidula</i>
	<i>Clausilia bidentata</i>	<i>Clausilia bidentata</i>	<i>Clausilia bidentata</i>	<i>Clausilia bidentata</i>
	<i>Pomatias elegans</i>	<i>Pomatias elegans</i>	<i>Pomatias elegans</i>	
	<i>Spermodea lamellata</i>	<i>Spermodea lamellata</i>	<i>Spermodea lamellata</i>	
	<i>Oxychilus navarricus</i>	<i>Oxychilus navarricus</i>	<i>Oxychilus navarricus</i>	
	<i>Hygromia limbata</i>	<i>Hygromia limbata</i>	<i>Hygromia limbata</i>	
	<i>Balea perversa</i>	<i>Balea perversa</i>	<i>Balea perversa</i>	
	<i>Azeca goodalli</i>		<i>Azeca goodalli</i>	
	<i>Leiostyla anglica</i>		<i>Leiostyla anglica</i>	
	<i>Macrogastra rolpheii</i>		<i>Macrogastra rolpheii</i>	
	<i>Zonitoides excavatus</i>		<i>Zonitoides excavatus</i>	
	<i>Zenobiella subrufescens</i>		<i>Z. enobiella subrufescens</i>	
			<i>Acicula fusca</i>	
			<i>Vertigo alpestris</i>	
		<i>Ashfordia granulata</i>		
		<i>Lauria cylindracea</i>		
Extinct	<i>Neniatlanta pauli</i>			
	<i>Zonitoides sepultus</i>			
	<i>Aegopinella bourdieri</i>			
	<i>Retinella elephantium</i>			
	<i>Aegopsis acieformis</i>			
	<i>Bradybaena chouquetiana</i>			

Their occurrence within modern Polish forests is indicated (after Cameron & Pokryszko, 2004; Cameron *et al.*, 2010).

itself) and no extinct species occur (Table 2). Although the Eemian fauna is less rich than those from MIS 11, it does contain several Eastern and Central European species, including one (*Daudebardia rufa*) that is unrepresented in the earlier faunas. Some species, such as *Acicula fusca* and *Pomatias elegans*, occur in the Condat tufa but do not reach northern France during the Eemian optimum (MIS 5e), although both species occur at more northern sites during the Holocene.

The forest faunas from the Holocene are also less rich than those from MIS 11. They differ from the assemblages of MIS 11 and MIS 5e in containing fewer species with Central and East European modern ranges but Western European species are well

represented and include two species (e.g. *Vertigo alpestris* and *Ashfordia granulata*) absent in the earlier interglacial assemblages (Table 2). Although not apparent from the list in Table 2, *Spermodea lamellata* and *Leiostyla anglica*, two species with Western European ranges, are much more frequent in Holocene tufas than in those of interglacial age.

Despite the inferior quality of the records from MIS 9 and MIS 7, it is nevertheless clear that Pleistocene interglacial forest malacofaunas from NW Europe are richer in species than those from either the Holocene or modern assemblages. This enhanced interglacial richness resulted from the occurrence of several species that are now extinct or that live today further east and south, and

never reached the western limits of Europe either during the Holocene or at the present day. As a consequence of this interglacial influx of Eastern and Southern elements, Pleistocene faunas from NW Europe shared many species in common with modern forest faunas from Central Europe (Cameron & Pokryszko, 2004; Cameron *et al.*, 2010).

In order to shed light on the underlying causes of such faunal differences, stable isotope analyses have been undertaken through several of the critical tufa profiles. These have enabled estimates of temperature and moisture to be calculated from identical profiles yielding the malacological records (Dabkowski *et al.*, 2011, 2012). Temperatures during MIS 11 appear to have been the highest, but the temperature values for MIS 5e emerge as rather similar to those of the Holocene sites studied. Moisture values, on the other hand, appear to have been much higher during the thermal optimum of both Pleistocene interglacials, compared with that of the Holocene. Increased aridity during the Holocene optimum thus appears to have been a significant factor, preventing the spread of these more sensitive species. A similar decrease of land snail diversity from Middle Pleistocene interglacials to the Holocene has been reported from Thuringia in Germany (Mania, 1995b). Here the decline relates mostly to species that currently inhabit the Mediterranean region. No direct records of temperature and humidity are available from these German sites, but it seems likely that this decline also resulted from similar climatic causes.

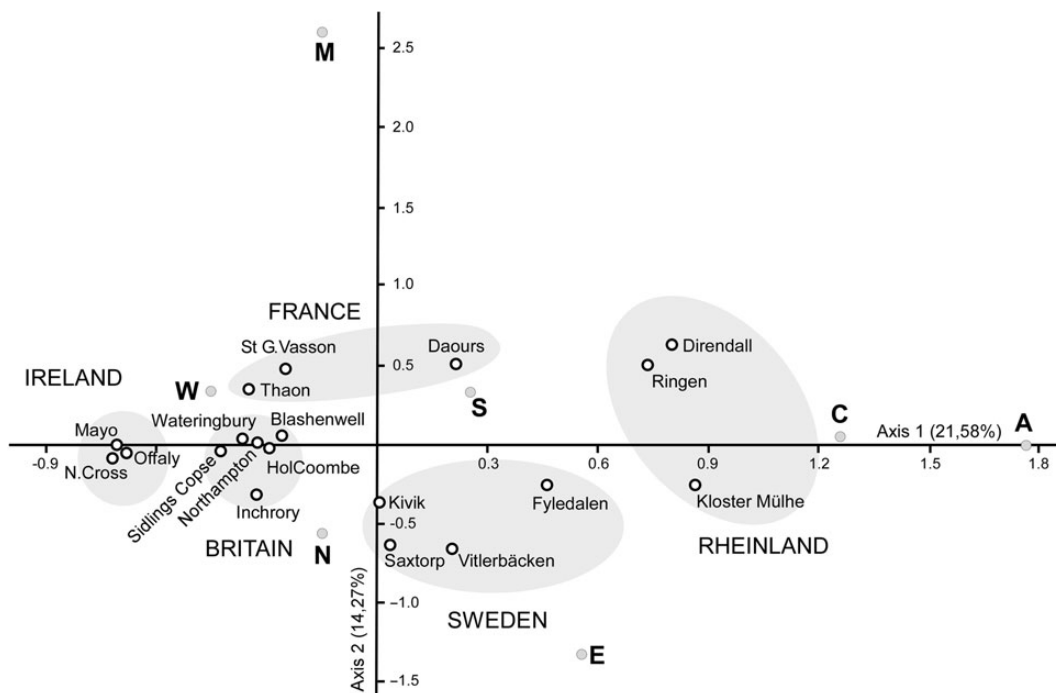
In order to explore the regional differentiation of Holocene faunas, eight additional sites from more northern regions (Ireland, Scotland and Sweden) were added to the Holocene database to extend the geographical coverage. A CA was undertaken on data from these 19 Holocene tufas, which cover a relatively large part of NW Europe (Table 1; Fig. 1). The first two axes of the ordination explain 34% of the total variance (Fig. 6). The assemblages fall into a series of five distinct clusters that largely relate to their position on a west-east transect. This presumably reflects some influence of ‘continentality’, perhaps increasing susceptibility to frost and prolonged winter cold (cf. Kerney, 1968). As expected, the

land snail assemblages from Ireland, Britain and northern France are characterized by higher frequencies of Western species, whereas this element is missing from the assemblages from Sweden and the Rheinland, which both contain higher frequencies of species from Central and Eastern Europe (Fig. 6).

Land snail assemblages from the Irish Holocene contain no unique elements (*Zenobiella subrufescens* does occur in Holocene tufas from western Britain but at none of those reviewed here) and are a subset of species found in Britain. There is nothing to suggest that this faunal impoverishment is linked to the flooding of the Irish Sea, since many of the forest species appeared in Ireland during the mid Holocene, long after any possible land-bridge existed (Preece *et al.*, 1986a). Indeed, the land snail successions from the Irish Holocene are little different from those from Britain. It would appear that most of the ‘lusitanian’ elements, such as *Semilimax pyrenaicus* and *Geomalacus maculosus*, present in the modern Irish biota result from introductions in relatively recent times (cf. Beatty & Provan, 2012).

Britain, however, does not represent a subset of species found in northern France, but contains a few elements (e.g. *S. lamellata*) yet to be discovered in the Holocene of NW Europe. *Leiostylis anglica*, as its name implies, is relatively frequent as a Holocene fossil in Britain, but is known from only a single site in France (Limondin-Lozouet & Preece, 2004). However, this might result from sampling bias as relatively few Holocene tufas have been studied in France. Moreover, *L. anglica* has recently been found living in the Pas-de-Calais region of northern France (Cucherat, 2004). Several species, such as *Azeca goodalli*, are much more common in Holocene tufas in France than they are in those from Britain, whereas *Helicodonta obvolvata*, *Oxychilus navarricus*, *Sphyradium doliolum* and *Hygromia limbata* are not known from any Holocene tufa in Britain. Since most of these species do not appear until after ~6 ka BP in northern France, it is possible that their absence from British Holocene sites might be linked to Britain’s newly acquired island status.

A much debated topic in Holocene palaeoecology is the evidence for a thermal maximum (0.5–1.5°C above the



**Figure 6.** A correspondence analysis undertaken on the 19 Holocene tufas considered (Fig. 1 and Table 1). The data plot along a west-east axis, which is presumably linked to a continentality gradient. See details in caption of Figure 3.

pre-industrial level) that occurred in NW Europe between 7 and 5 ka BP as indicated by a range of proxy records (Renssen *et al.*, 2012). At this time a number of thermophilous species of plants and animals lived at locations considerably beyond their present ranges. Distributional contractions after 5 ka BP are shown by a number of species of land snail and some of these have been attributed to climate deterioration following the thermal maximum (Kerney, 1968). The distribution maps in the British nonmarine molluscan atlas (Kerney, 1999), where fossil records are plotted with modern ones, provide clear evidence of faunal changes. Many of these fossil records relate to land snails from Holocene tufa sequences. The obvious question to address is whether the forest snail assemblages of the mid Holocene were richer than those from forest environments in the same region today.

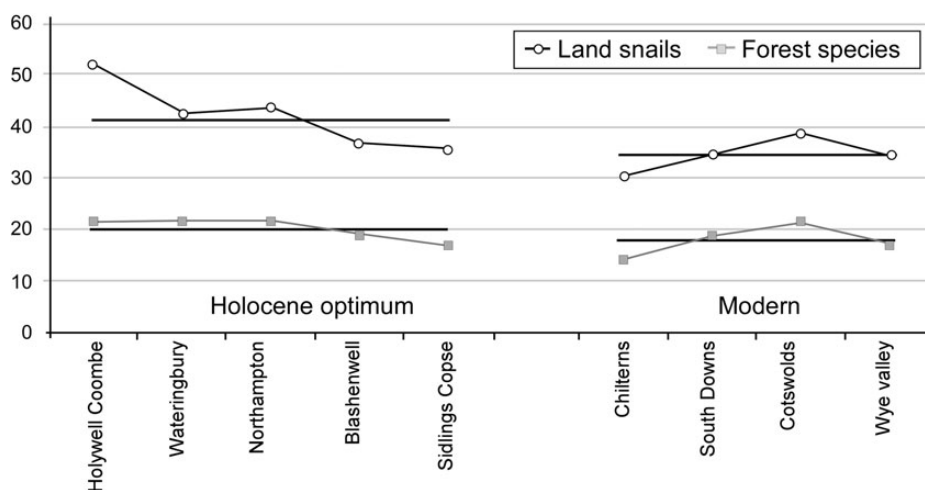
The sampling of land snail communities in modern forest and fossil forest assemblages from tufa sequences is fundamentally different. In the first instance, the sampling is undertaken over a larger spatial area (e.g. 400 m<sup>2</sup>) and involves both searching by eye and the sieving of leaf litter and soil in order to obtain more complete faunal inventories (e.g. Cameron & Pokryszko, 2005). Palaeontological sampling relates to the assemblages that occurred at a single spot, but they may not have existed at precisely the same time. Rates of tufa accumulation can be calculated if the profile has been radiocarbon-dated (e.g. Preece & Day, 1994; Limondin-Lozouet & Preece, 2004) and it is then possible to establish the temporal resolution of each sample. Although rates of tufa growth vary, such studies suggest that typical sampling of a tufa profile (e.g. every 5 cm), produces samples that cover multidecadal to centennial timescales. This time-averaging compensates for the differences in the spatial sampling and is not thought to be a serious impediment to meaningful comparisons between fossil and modern faunas (but see discussion by Cernohorsky, Horsák & Cameron, 2010).

Figure 7 plots both the total number of land snail species and the number of forest species recovered from samples dating from the 'Forest optimum' of five Holocene tufas in southern England alongside comparable data from modern woodland from the same general region. In both sets of data *Ceciloides acicula* has been excluded because of its subterranean habit (see above). In their study of the land snail faunas from calcareous woodlands in southern England, Cameron *et al.* (2006) found that the richest sites occurred in the Cotswolds, where the total number of species recorded from the region was 39. However, individual

sites in this region never yielded more than 35 species. Moreover, this total included species such as *Monacha cantiana* and *Oxychilus navarricus*, which are relatively recent introductions. Of the 39 species, 21 belong to the 'forest' group, but no individual Cotswold site yielded more than 19 species of forest snails. The richest Holocene succession was Holywell Coombe, Folkestone, which yielded up to 51 species during the climatic optimum, including 21 species of forest snails. Several different tufa profiles were analysed from different parts of this dry valley, so this high total, in part, reflects the intensity of work undertaken at this site (Preece, 1998; Preece & Bridgland, 1999).

The land snail assemblages from the Holocene tufas emerge as both richer in overall species (mean = 41) and in the frequency of forest species (mean = 20), compared with data from modern forest faunas (mean number of total species = 34; mean number of forest species = 18). Species such as *Vertigo pusilla*, *V. alpestris*, *L. anglica* and *S. lamellata* were all more widespread during the mid Holocene (Kerney, 1999) and this combination of species is not known from any single site in southern Britain today (Cameron *et al.*, 2006). At some sites, such as Wateringbury, Kent, there is clear evidence for declines in some of these species towards the top of the tufa sequence (Kerney *et al.*, 1980), but no suggestion that this was linked to human disturbance because the habitat remained forested. Neither is it easy to relate the declines in *L. anglica* and *S. lamellata* to a climatic cause because they do not coincide with marked changes in the associated records of stable isotopes and trace elements (Garnett *et al.*, 2004). However, this does not mean that climate, or some indirect effect of climate, is not implicated. Further work is needed at more tufa sites to resolve this issue.

This preliminary assessment of the diversity of land snails during different temperate stages has revealed some interesting patterns. While the general pattern of malacological colonization during each interglacial shows broad similarities (Limondin-Lozouet, 2011), the details vary and impart a particular faunal 'signature' characteristic of each temperate period. There seems to have been a general decline in species richness through the Middle and Late Pleistocene, and even an appreciable decline since the mid Holocene. These declines appear to have taken place without human intervention, suggesting that climatic influences may have been involved, although further work is needed to corroborate this suggestion. More sites need to be added to the database to establish the veracity of the broad patterns discussed here.



**Figure 7.** Plots of total number of land snails and number of forest species recorded at mid Holocene sites during the climatic optimum (between ~9 and 6 ka) compared with data from modern calcareous woodland in southern England (Cameron *et al.*, 2006). The horizontal black lines indicate the mean values.

## CONCLUSIONS

This paper provides an historical perspective on the development and composition of forest snail assemblages in NW Europe. Several points emerge from our analyses of the molluscan record from Quaternary tufas and that derived from modern communities.

(1) NW European land snail faunas were significantly richer during Pleistocene interglacials than they were during the Holocene.

(2) Several of these interglacial periods (particularly MIS 11 and MIS 5e) exhibit a distinctive malacological signature, reflected by a combination of extinct species and those that occurred far beyond their present geographical ranges.

(3) Greater species richness during Pleistocene interglacials resulted from an expansion of species from Central and Southern Europe into the westernmost parts of Europe. These species are absent during the Holocene. The Pleistocene interglacial land snail faunas from Western Europe therefore shared several species in common with modern forest faunas from Poland. This was particularly evident during MIS 11 (424–374 ka) and to a less extent during the Eemian (MIS 5e, 130–116 ka).

(4) Comparison of Holocene land snail successions with those of earlier interglacials suggests that any influx of species from Eastern Europe should already have occurred by the mid Holocene. Their absence during the Holocene cannot, therefore, be attributed to human influence but is more probably linked to climate change, perhaps increased aridity.

(5) A CA of all the 19 Holocene tufa sequences produced geographical clusters that clearly relate to their position on a west-east transect. Irish assemblages contain no unique elements and are a subset of species found in Britain. Britain, however, does not represent a subset of species found in northern France, but contains a few elements (e.g. *Spermodea lamellata*) yet to be discovered in the Holocene of NW Europe. However, French Holocene tufas contain several species (e.g. *Helicodonta obvoluta*, *Oxychilus navarricus*, *Sphyradium dolium* and *Hygromia limbata*) that are rare or completely unknown from British tufas of the same age.

(6) The land snail assemblages from mid Holocene tufas exceed those from the richest woodland sites in Britain today. Species such as *Vertigo pusilla*, *V. alpestris*, *Leiostryla anglica* and *Spermodea lamellata* were all more widespread during the mid Holocene and nowhere can they all be found together at a single site in southern England today. This general pattern may hold true of other sites in NW Europe.

This paper provides a preliminary synthesis of the changes in land snail diversity through time in NW Europe. The results show that most thermophilous species extended their geographical ranges considerably during temperate periods and that many species with modern Central and Southern European distributions once inhabited more northern regions. More malacological successions are needed to establish the generality of the observed patterns both for the Holocene and especially during earlier interglacials. More quantitative studies of modern forest faunas would also enable further comparisons and allow more detailed assessments of changes in snail diversity and distribution that have occurred since the mid Holocene, resulting from both 'natural' and anthropogenic causes.

## SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies*.

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