



HAL
open science

What do Lateglacial and Holocene land snail communities tell us about the palaeoenvironments of Mediterranean France?

Frédéric Magnin, Sophie Martin, Vincent Ollivier, Naïs Sirdeys

► **To cite this version:**

Frédéric Magnin, Sophie Martin, Vincent Ollivier, Naïs Sirdeys. What do Lateglacial and Holocene land snail communities tell us about the palaeoenvironments of Mediterranean France?. *Boreas*, 2024, 10.1111/bor.12681 . hal-04781914

HAL Id: hal-04781914

<https://amu.hal.science/hal-04781914v1>

Submitted on 14 Nov 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License



What do Lateglacial and Holocene land snail communities tell us about the palaeoenvironments of Mediterranean France?

FRÉDÉRIC MAGNIN , SOPHIE MARTIN , VINCENT OLLIVIER  AND NAÏS SIRDEYS 

BOREAS



Magnin, F., Martin, S., Ollivier, V. & Sirdeys, N.: What do Lateglacial and Holocene land snail communities tell us about the palaeoenvironments of Mediterranean France? *Boreas*. <https://doi.org/10.1111/bor.12681>. ISSN 0300-9483.

Southeastern France occupies a key biogeographical position on the lower Rhone corridor, at the interface between southern and northern Europe. It is also at the heart of long-standing ecological debates about the respective roles of natural and human drivers in shaping the Mediterranean landscape. Molluscan analysis may represent a valuable contribution to this issue. In this paper, land snail assemblages from three calcareous tufa deposits in the Luberon mountain were used to reconstruct Lateglacial and Holocene palaeoenvironments. The Lateglacial communities only differ from the Pleniglacial ones by the development of hygrophilic snails. We note a high moisture budget at the end of the Lateglacial Interstadial (LGI). A patchy, steppe landscape is attested. A time lag in recolonization by woodland species during the LGI is conceivable. The postglacial woodland assemblages then trace a laborious reassembly of forest snail communities. It takes place mainly between *c.* 8000 and *c.* 6600 cal. a BP with spatial disparities and delayed recruitments. The French Mediterranean region has not benefitted from the macrorefugia that it would have sheltered or with which it would have been close. Woodlands, however, appear progressively more closed and complex *c.* 8000 cal. a BP. They reached their optimum *c.* 7500 to 7400 cal. a BP although their canopy seems to have stayed quite open. Anthropization remained weak during the Early Neolithic. A significant woodland opening is observed in the Early–Middle Neolithic. Human impact becomes clear from the Late Neolithic. Nevertheless, there are substantial differences compared with Basse-Provence, where a more marked openness of the landscape from 7000 cal. a BP was accompanied by the development of Mediterranean synanthropic snails. The molluscan successions of the Luberon mountain should be a reference for the development of the Lateglacial and Holocene malacofauna in the SE of France, at the northern boundary of the western Mediterranean domain.

Frédéric Magnin (frederic.magnin@imbe.fr), Aix Marseille Université, Avignon Université, CNRS, IRD, IMBE, Technopôle de l'Environnement Arbois-Méditerranée, BP 80, 13545 Aix-en-Provence Cedex 4, France; Sophie Martin, Inrap Méditerranée, Rue de l'Acropole, 34420 Villeneuve-les-Béziers, France and ASM, UMR 5140 CNRS, Université Paul-Valéry Montpellier 3, Montpellier, France; Vincent Ollivier, CNRS, Aix Marseille Université, Ministère de la Culture, LAMPEA, UMR7269, 5 rue du Château de l'Horloge, 13097 Aix-en-Provence Cedex 2, France and Aix Marseille Université, CNRS, FRECCOREV, Aix-en-Provence, France; Naïs Sirdeys, Aix Marseille Université, CNRS, IRD, INRAE, CEREGE, Aix-en-Provence, France and CNRS, Aix Marseille Université, Ministère de la Culture, LAMPEA, UMR7269, 5 rue du Château de l'Horloge, 13097 Aix-en-Provence Cedex 2, France; received 12th July 2024, accepted 11th October 2024.

Mediterranean France is a key region to study the postglacial recolonization by terrestrial molluscs in a fragile geosystem progressively shaped by a fluctuating climate and a long history of human land use. The relevance of this region lies in its properties as an ecotone between Mediterranean and temperate Europe and as a complex crossroads of recolonization routes from glacial refugia, of colonization and exchanges by human groups and of natural as well as human-mediated dispersal of snails (Germain 1930; Blondel *et al.* 2010; Binder *et al.* 2017; Battentier *et al.* 2018).

The terrestrial malacofauna between the eastern Pyrenees and the Ligurian Alps presents a high level of endemism (Falkner *et al.* 2002; Gargominy *et al.* 2011). Holyoak (1989) suggested that the modern ranges of extremely localized woodland species in this area could indicate the likely location of glacial refugia. Médail and Diadema (2009) have located there three putative glacial refugia for cold-sensitive plants. The French Mediterranean region is also at the crossroads of recolonization routes from two major refugia, i.e. the Iberian and Italian peninsulas, which contributed to the repopulation of

northern parts of Europe by various organisms (Huntley 1988; Hewitt 1996, 1999; Preece 1997; Taberlet *et al.* 1998; Michaux *et al.* 2003; Limondin-Lozouet & Preece 2014). Although there is accumulating evidence for the existence of scattered cryptic refugia or micro-refugia (Ant 1966; Bilton *et al.* 1998; Stewart & Lister 2001; Pfenninger *et al.* 2003; Schmitt & Varga 2012; Salvi *et al.* 2013; Juříčková *et al.* 2014; Fiorentino *et al.* 2016; Kühne *et al.* 2017), the paradigm of postglacial recolonizations from southern macrorefugia remains well established (Vialatte *et al.* 2008). It is therefore essential to seek fossil evidence in favour of one or the other of these recolonization processes (Horsák *et al.* 2019).

In the Mediterranean region, it quickly becomes difficult to distinguish the respective impacts of climate and human activities (Roberts *et al.* 2011), as in the case of interpreting Holocene molluscan assemblages (Martin 2004; Magnin & Martin 2008; Magnin *et al.* 2022). The settlement of the first agropastoral societies in SE France is dated between 5826 and 5470 cal. a BCE (Binder *et al.* 2017). The Neolithic Culture first

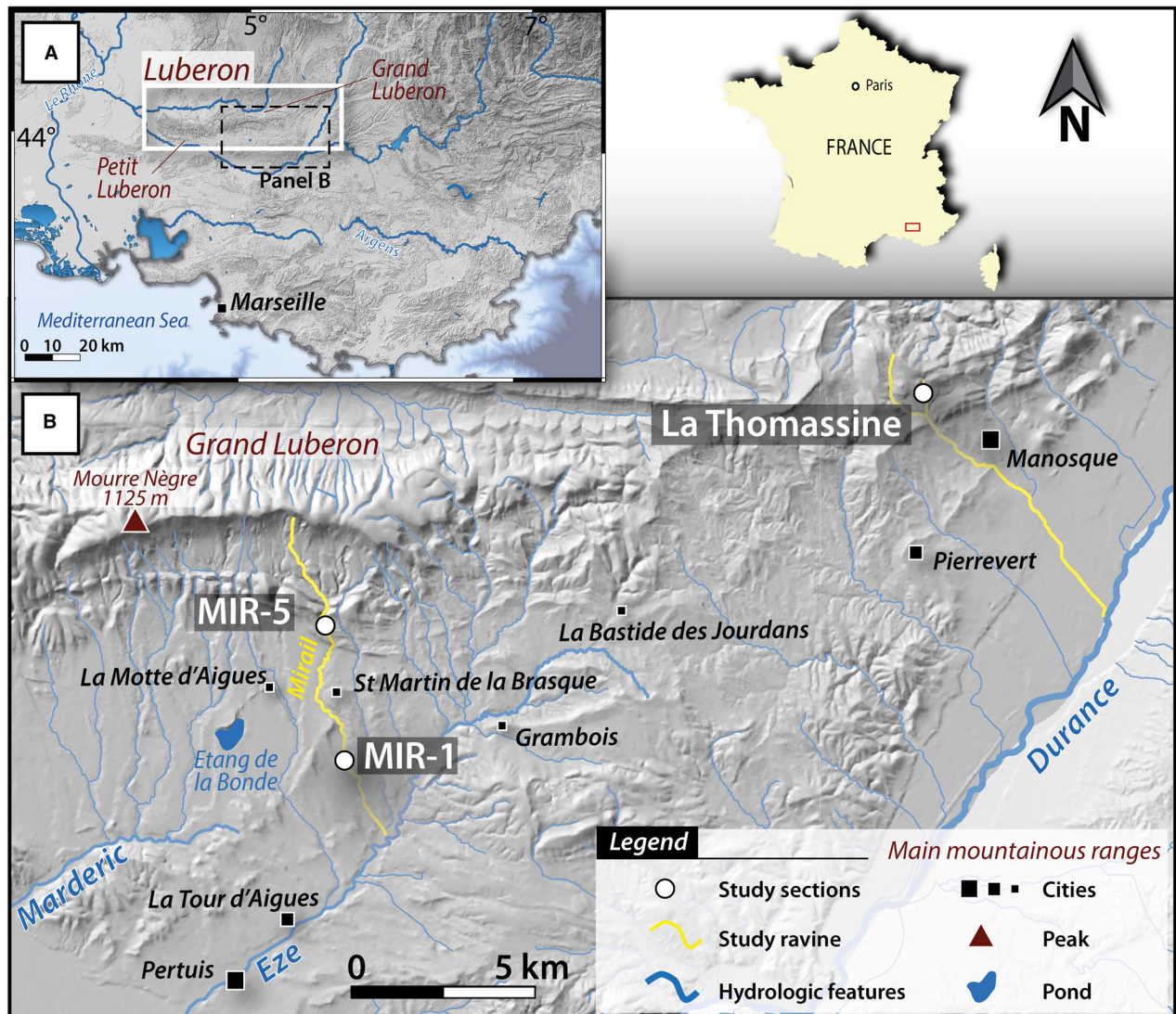


Fig. 1. Maps showing the location of the Luberon mountain (A) and of the three study sites (B): La Thomassine, MIR-1 La Stèle and MIR-5 Le Verger.

concerned the coast before spreading into the hinterland. Although the various stages of anthropogenic alterations regarding the composition of the vegetation are well documented, the consequences of human impact in terms of stand and landscape structures still are in debate (Battentier 2022). Molluscs may represent a useful independent source as a proxy for past forest structure (Mitchell 2005). They are reliable indicators of the structure of both current plant stands and the landscape (Magnin *et al.* 1995; Magnin & Tatoni 1995; Labaune & Magnin 2001).

In the Mediterranean lowlands of Languedoc and western Provence, actual woodland snail assemblages are rare during the Holocene (Magnin 1991; Martin 2004; Magnin *et al.* 2022). Anthropization not only has altered landscape and snail habitats, but snail communities have

also been deeply modified by human-mediated dispersal of species (Aubry *et al.* 2005; Magnin & Martin 2012; Magnin *et al.* 2022). It is, however, essential to investigate the extent to which the intensity and precocity of the anthropization, so far revealed by malacological analyses, are not geographically circumscribed. Anthracological analysis indeed has highlighted significant regional disparities in vegetation dynamics during the Holocene (Battentier *et al.* 2018; Battentier 2022).

The present study on the Luberon aims to extend malacological investigations towards the border of the Mediterranean lowlands. Located at the boundary between Basse-Provence and Southern Alps (Fig. 1), this mountain offers a mixture of Alpine and Mediterranean characteristics (Ollivier *et al.* 2014). Quaternary deposits are abundant, including thick postglacial

calcareous tufas (Ollivier 2006). This type of sediment is considered as one of the most suitable for palaeoecological investigations owing to the many proxies it preserves, including shells of continental molluscs (Alexandrowicz 2004; Granai *et al.* 2020). Furthermore, molluscs appear to be a valuable data source in this region where most of the pollen sequences are difficult to interpret, mainly on account of bad pollen preservation (Beaulieu *et al.* 2005). This is why the present work is based on snail assemblages contained in tufa deposits with the aims (i) to define Lateglacial and Postglacial snail communities and their environmental significance, (ii) to reconstruct the postglacial reassembly of woodland snail communities and compare it with that of temperate Europe, (iii) to question the structure and nature of Holocene woodlands and (iv) to look for the imprint of human activities on snail communities and their habitats.

Regional setting and study sites

The three studied successions are located in the Luberon Regional Natural Park (Fig. 1). The Luberon is a calcareous mid-mountain which stretches from west to east for more than 60 km. It marks the boundary between Basse-Provence to the south and Haute-Provence to the north. Our study focuses on the Grand Luberon and its eastern end, the Luberon de Manosque. The altitude of Grand Luberon Mountain (1125 m a.s.l.) is sufficient to produce a bioclimatic layering from the meso-Mediterranean to the supra-Mediterranean level (CNRS, ER 30 1975; Dumas 2013). Its southern foothills extend widely to the Durance River. The Luberon de Manosque is lower (790 m a.s.l.).

Two of the three sections analysed (Fig. 1) are located in the Mirail valley, on the southern foothills of the Grand Luberon, next to La Motte d'Aigues (Vaucluse). Situated on the right bank of the river, at *c.* 400 m a.s.l., MIR-1 La Stèle (43.755922°N, 5.547115°E) represents the oldest Lateglacial part of Le Mirail tufas (Ollivier 2006). Located downstream from the Mirail karstic source and upstream from the previous section, MIR-5 Le Verger (43.787462°N, 5.541658°E) is a thick Lateglacial and Holocene deposit. The third section is located near Manosque (Alpes-de-Haute-Provence), in the eastern part of the Luberon: La Thomassine (43.849887°N, 5.753327°E). This Holocene section is situated at ~500 m a.s.l. in a ravine that cuts deeply into marl formations.

Material and methods

Radiocarbon dating

Data on radiocarbon dating are listed in Table 1. Dates judged admissible are plotted on the stratigraphic

sections (Fig. 2). Where possible, radiocarbon dates were measured on charcoal. Otherwise, they were measured either on minute shells, selecting species as much as possible to avoid the limestone effect (Brennan & Quade 1997; Pigati *et al.* 2004, 2010, 2013, 2015), or on earthworm granules (Moine *et al.* 2017). Radiocarbon dating was conducted by Poznan Radiocarbon Laboratory, Poznan, Poland, by Beta Analytic laboratory, Miami, USA, and by Centre de datation par le radiocarbène, Lyon, France. The dates were calibrated using the IntCal20 calibration curve (Reimer *et al.* 2020) and the program PAST 4.13 (Hammer *et al.* 2001). Several dates are not satisfactory. That of MIR-1 (8), measured on *Jaminia quadridens* for want of a better alternative, is affected by a significant limestone effect. The date obtained for MIR-1 (5c) on *Succinella oblonga* appears to be too young, for no obvious reason. The amount of carbon available for MIR-1 (6d2) was small but the date is not significantly impacted. No age–depth model was proposed owing to the heterogeneous deposits studied, with variable and unpredictable sedimentation rates and undetectable hiatuses.

Molluscan analysis

Samples of sediment of 10 L each were collected at non-equidistant intervals according to the sedimentary characteristics of the deposits. Each corresponds to a thickness of about 10 cm. Consolidated tufas and excessively stony sediments were generally not sampled. The samples were processed following standard methods (Evans 1972; Puisségur 1976). For each taxon of each assemblage, the minimum number of individuals includes the number of unbroken shells augmented by the greatest number of identifiable fragments, either apical or apertural. We listed the species for which a minimum number of individuals could not be determined. In the case of *Pisidium*, the number of valves was reduced by half. The taxonomic nomenclature follows that of Welter-Schultes (2012), occasionally revised (Tables S1–S3). We have given up on identifying the *Euconulus* (*Euconulus fulvus* and *Euconulus alderi*). The same applies to two Vitrinids (*Vitrina pellucida* and *Phenacolimax major* = Vitrinidae sp. indet.) while a third, *Oligolimax annularis*, is easier to distinguish. In 2015, we reported the presence of *Vitrea* cf. *etrusca* (Paulucci 1878) in the Thomassine tufa. This snail has since been described as *Vitrea luberonensis* (Magnin 2023a, b).

The Holocene portion of the MIR-5 section was first studied by Martin (2004). The data were revised and supplemented with the Lateglacial part of the section. The Thomassine section had been the subject of a preliminary study (Ollivier *et al.* 2015). Sampling was completed and malacofauna revised. All the results are presented in diagrams showing for each assemblage the frequency of each species expressed as a percentage

Table 1. Radiocarbon dates for MIR-1 (Mirail La Stèle), MIR-5 (Mirail Le Verger) and THOM (La Thomassine).

Section	Sample	Laboratory code	Material	Radiocarbon age (a BP)	Radiocarbon age (cal. a BP 2σ)	Comments and references	
MIR-5 Le Verger	MIR-5 (14)	AA42670	Charcoal (non-AMS)	4536±56	5421–4989	Ollivier (2006)	
	MIR-5 (11a)	AA42671	Charcoal (non-AMS)	4737±47	5577–5331	Ollivier (2006)	
	MIR-5 (8c)	Lyon 10 574	Charcoal (non-AMS)	6550±95	7592–7275	Ollivier (2006)	
	MIR-5 (2b)	Lyon 10 522	Charcoal (non-AMS)	7775 ± 65	8760–8425	Ollivier (2006)	
	MIR-5 (1b)	Beta-616 358	Charcoal (AMS)	10 960±30	12 983–12 770		
	MIR-5 (–1)	Poz-132 619	Charcoal (AMS)	11 260±60	13 289–13 094		
	MIR-5 (–3)	Poz-132 618	Charcoal (AMS)	11 370±60	13 383–13 134		
	MIR-5 (–9)	Poz-12 440	Charcoal (AMS)	11 620±60	13 589–13 346	Ollivier (2006)	
MIR-1 La Stele	MIR-1 (11)	Poz-12 435	Charcoal (AMS)	780±30	737–670	Ollivier (2006) (channel)	
	MIR-1 (8)	Beta-616 360	Shells (AMS) <i>Jamiania quadridens</i>	12 120±40	14 090–13 830	Probable limestone effect	
	MIR-1 (6d)	Beta-616 359	Shells (AMS) <i>Vallonia pulchella</i>	10 660±30	12 725–12 625		
	MIR-1 (6d2)	Poz-133 756	Shells (AMS) <i>Vertigo antivertigo</i>	10 380±60	12 562–11 971	Only 0.7 mg C	
	MIR-1 (5c)	Poz-133 757	Shells (AMS) <i>Succinella oblonga</i>	9860±50	11 446–11 203	Faulty dating, unknown reason	
	MIR-1 (3d)	Poz-133 758	Earthworm calcite granules (AMS)	12 520±60	15 075–14 364		
	MIR-1 (2)	Poz-7825	Charcoal (AMS)	12 640±60	15 242–14 677	Ollivier (2006)	
	THOM – La Thomassine	THOM-(8b)	Beta-646 475	Charcoal (AMS)	4240±30	4854–4656	
		THOM (7b)	Beta-616 357	Charcoal (AMS)	5600±30	6445–6309	
		THOM (7a)	Poz-69 478	Charcoal (AMS)	5790±35	6674–6496	Ollivier et al. (2015)
THOM (5b)		Beta-693 294	Charred seed (AMS) <i>Hordeum vulgare</i>	5920±30	6834–6671		
THOM (3b)		Poz-69 479	Charcoal (AMS)	6540±40	7555–7342	Ollivier et al. (2015)	
THOM (1b)		Beta-616 356	Charcoal (AMS)	6540±30	7551–7358		
	THOM-II (S2)	Beta-646 474	Charcoal (AMS)	7470±30	8362–8196		
	THOM-II (S1)	Beta-662 691	Charcoal (AMS) <i>Quercus</i> (deciduous)	7220±40	8161–7955		

of the total shells. This total excludes *Cecilioides acicula*, a burrowing species (Welter-Schultes 2012; Horsák et al. 2013). Species are arranged according to a combination of their ecological preferences and their order of appearance in the stratigraphy. For each section there is also a diagram showing the main characteristics of the assemblages and their composition by ecological groups. This approach by ecological groups should be seen as an approximation of the ecological reality intended to facilitate the communication of the results (Table S4). Although widely used, the method has never been found to be perfectly satisfactory (Cameron 1978; Evans 1991; Meyrick & Karrow 2007; Juříčková et al. 2014; Magnin et al. 2022), for species rarely fit strictly into any classification of that kind. It is necessary to discuss the meaning of certain species on a case-by-case basis, even if this flexibility may seem less rigorous. Mollusc assemblage zones have been indicated on the diagrams. The aim of this zonation is to facilitate the description of the stratigraphic distribution of assemblages in each succession. The zone boundaries were defined at first by eye (Meyrick & Karrow 2007; Magnin et al. 2022) and then using the CONISS algorithm with the help of Tilia software version 3.0.1 (Grimm 2011). The two methods yielded comparable

results. We have sometimes preferred zonation by eye for rare points of detail. Zones are noted in Roman numerals following the name of the site, e.g. THOM VI. Multivariate analysis, e.g. indirect ordination, is an interesting improvement because the assemblages are ordered only according to their taxonomic content, without *a priori* ecological knowledge. Correspondence analysis (CA; Greenacre 1984; Jongman et al. 1995; Legendre & Legendre 1998) is useful for exploring the structure of data tables. The CANOCO 4.5 package was used for computing CA and DCA (Ter Braak & Smilauer 2002). The results of these CAs are presented in Data S1, Figs S1–S3.

Results and interpretations

MIR-1 La Stèle

Stratigraphy. – The stratigraphy begins with a hydro-morphic sediment containing charcoals, and nodules related to secondary carbonation (Fig. 2). This set has more visible soil features in its upper part (level 2, 15 242 to 14 677 cal. a BP). A thick complex of tufa lays unconformably on the preceding ensemble. It starts before 15 075 to 14 364 cal. a BP. It shows oxidation

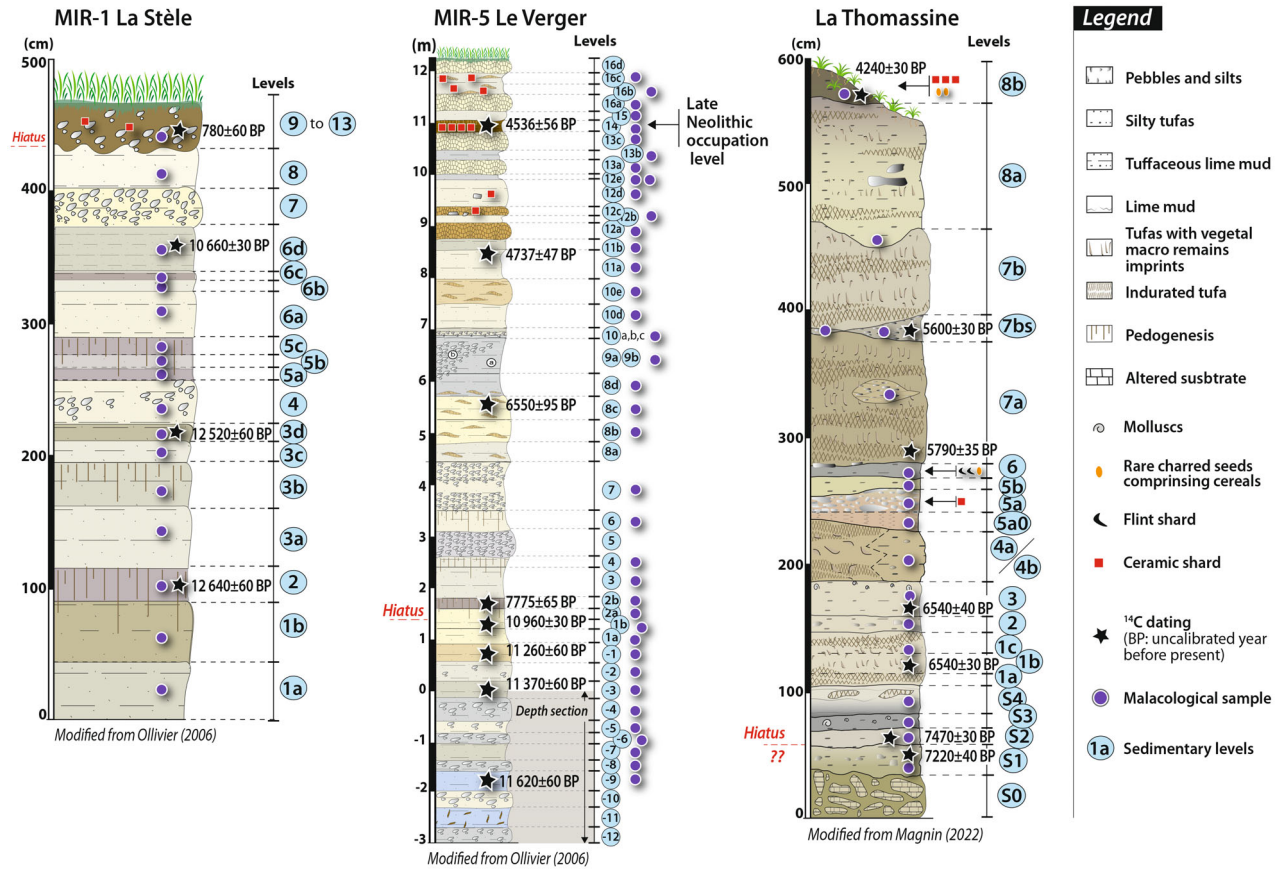


Fig. 2. Stratigraphy of the three studied sections (uncalibrated radiocarbon ages).

spots and pedomorphic traits. Two stony layers are interspersed in the tufa, the youngest (level 7) marking a significant break before a final level of tufa. The tufa formation corresponds, up to 6d, 12 725 to 12 625 cal. a BP, to the Lateglacial Interstadial (LGI). The upper stony layer (7) and the last tufa layer (8) are not satisfactorily dated.

Stratigraphic distribution of mollusc assemblages. – A total of 16 samples were taken (Fig. 2). The great poverty of samples 1a, 3a and 4 does not seem to be explained by weathering. The shells are not very abundant in general but there are considerable fluctuations (Table S1, Figs 3, 4).

Zone MIR-1 I (assemblages 1a and 1b). Assemblage 1b is dominated by *Xerocrassa geyeri*, *Vallonia pulchella* and *Galba truncatula*. We also find *Pupilla muscorum* f. *bigranata*, *Granaria variabilis* and *Abida secale* (*Clausilia rugosa* was present in 1a). This indicates a temporarily waterlogged grassland within a steppe landscape.

Zone MIR-1 II (2–3c). *Galba truncatula* indicates intermittent flooding. Hygrophilous snails are abundant

(*V. pulchella*, *S. oblonga*, small slugs). *Clausilia rugosa*, *X. geyeri* and *A. secale* form the second dominant group, which nowadays is found in grasslands and scrublands from the supra-Mediterranean level and above (Magnin 1989, 1991; Labaune & Magnin 2001, 2002). Malacofauna still indicates a juxtaposition of wet and dry grasslands in a cold environment.

Zone MIR-1 III (3d–5b). Species richness increases gradually. Aquatic (*G. truncatula*, *Pisidium* spp.) and marsh species (*Vertigo antivertigo*, *Oxyloma elegans*) are developing. *Vallonia pulchella* is regressing but other hygrophilous species are present (*S. oblonga*, *Cochlicopa lubrica*, *Vertigo pygmaea*). The part of the trio *C. rugosa*, *X. geyeri* and *A. secale* is reduced, but *G. variabilis* and *Punctum pygmaeum* are better represented. *Jaminia quadridens* and *Vallonia costata* have appeared. This zone is marked by the beginning of a significant development of open wetlands. The context probably is more temperate.

Zone MIR-1 IV (5c–6d). Aquatic and marsh species reach their maximum (*G. truncatula*, *Zonitoides nitidus*, *O. elegans*, *V. antivertigo*, *Vertigo moulinsiana*, *Vallonia*

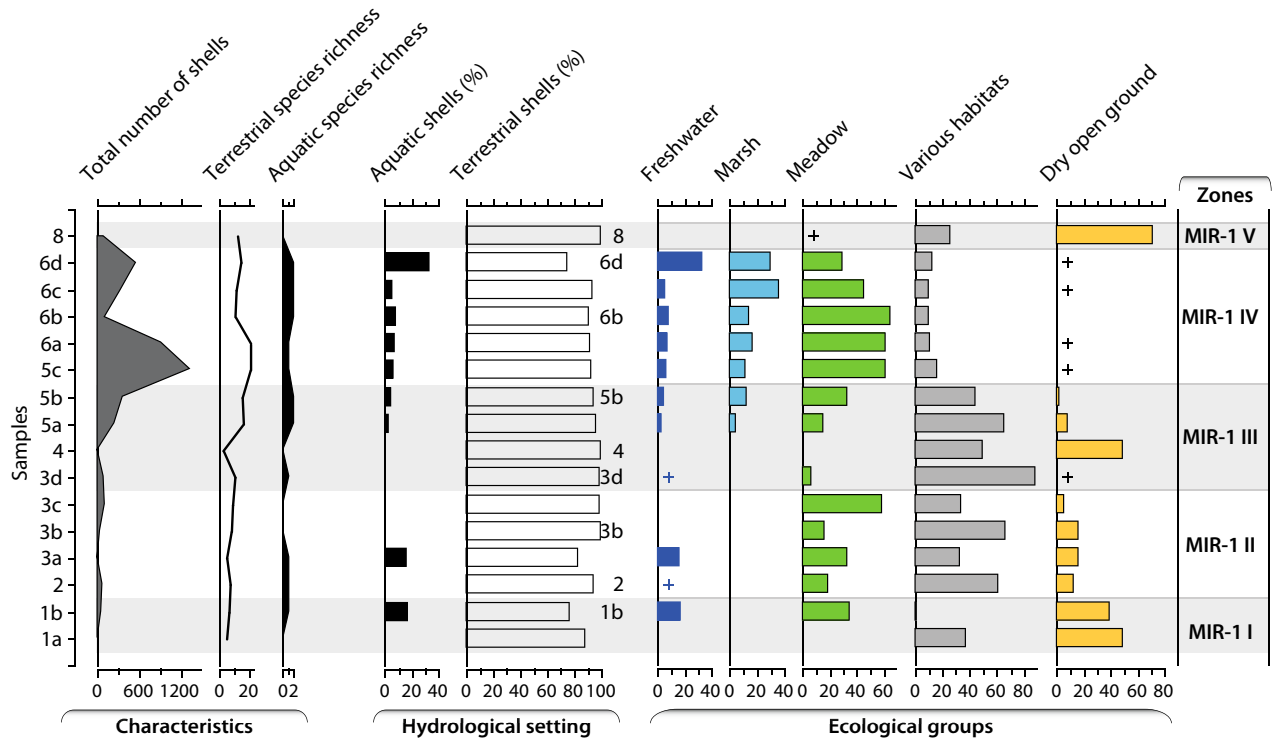


Fig. 3. Mir-1 La Stèle molluscan succession. Assemblage characteristics and ecological groups. Plus signs = values less than 1.3%.

enniensis and *Carychium minimum*). The wet meadow species *V. pulchella* suddenly shows considerable numbers. It is accompanied by *S. oblonga* and *C. lubrica*. A new xerophilous species (*Truncatellina callicratis*) and *Cepaea nemoralis* have appeared. The marsh has grown

considerably. However, there are dry grasslands nearby. Signs of a warmer climate appear to be confirmed.

Zone MIR-1 V (8). The change is dramatic. There are almost no more wetland molluscs. The assemblage is

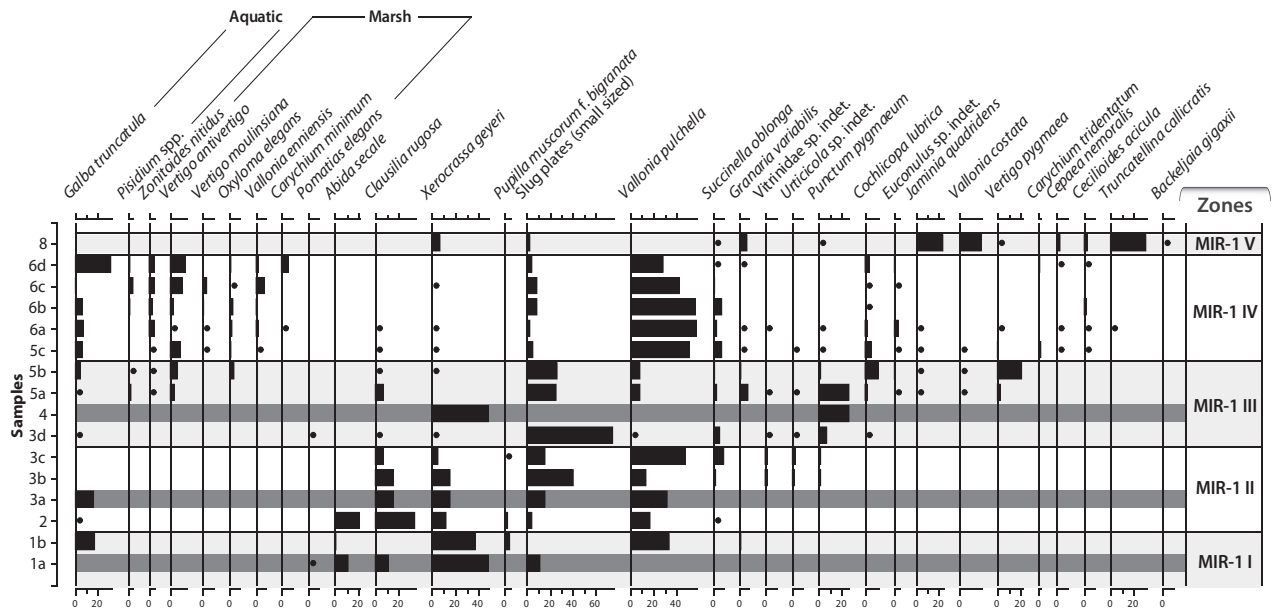


Fig. 4. Mir-1 La Stèle molluscan succession. Percentage histogram. Low abundance assemblages in dark grey. Dots = values less than 1.3%.

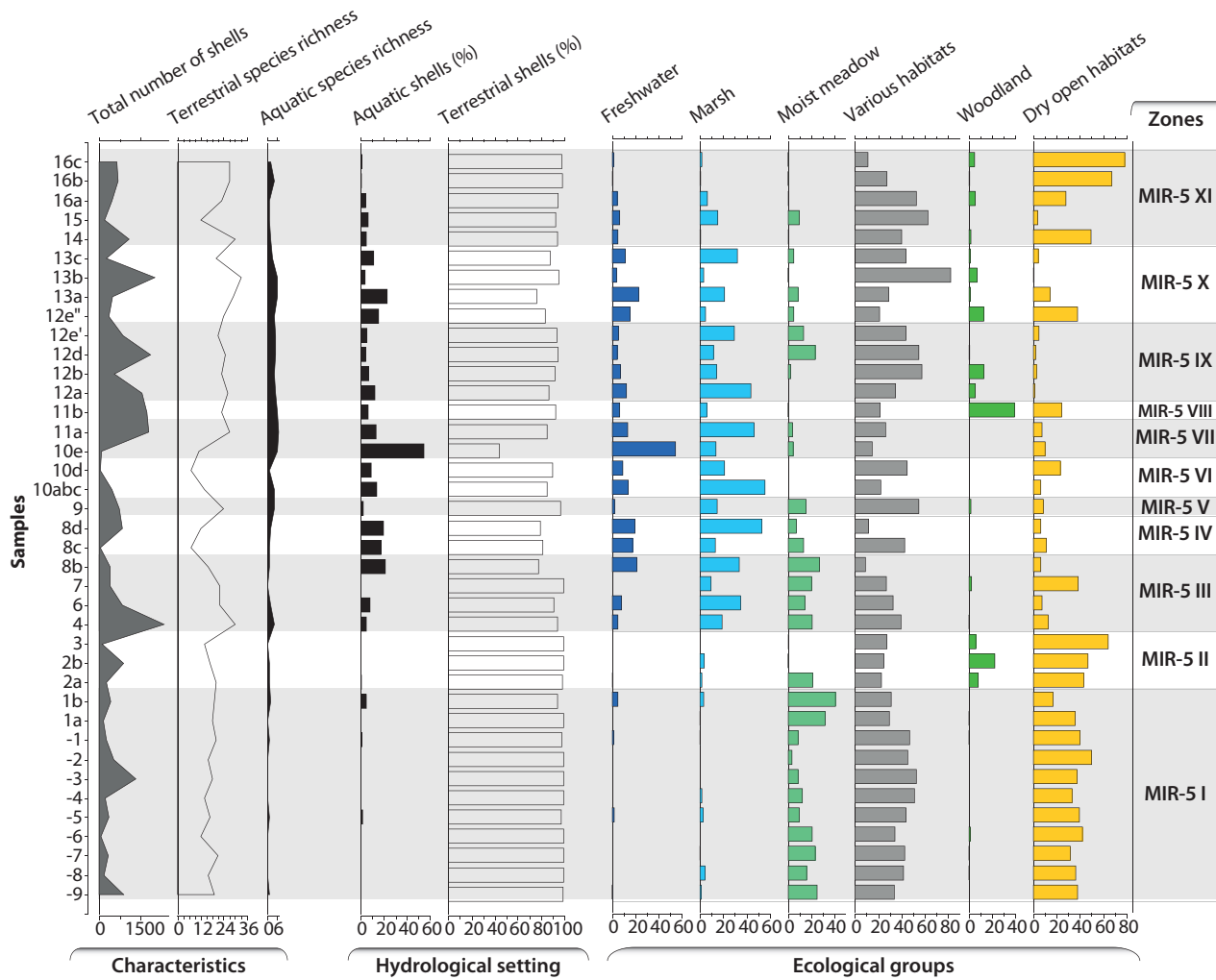


Fig. 5. Mir-5 Le Verger molluscan succession. Assemblage characteristics and ecological groups.

dominated by *T. callicratis*, *J. quadridens* and *V. costata*. In addition to these three species, there are *G. variabilis* and *X. geyeri*. Rare fragments attributable to the cold sensitive species *Backeljaia gigaxii* give this xerophilic assemblage a temperate climate nature.

Sketch of environmental changes at Le Mirail MIR-1 La Sièle. – At the base of the succession, the local environment is a wet grassland intermittently waterlogged (assemblages 1a–3c, between *c.* 15 000 and *c.* 14 800 cal. a BP). There are a number of species common in western Provence, both in Pleniglacial deposits and nowadays in open landscapes from the supra-Mediterranean level and above (Magnin 1989, 1991; Labaune & Magnin 2001). The onset of travertine facies (from 3a) does not coincide with a notable change in malacological assemblages. A transition (3d to 5b) then shows the development of wetlands and the coexistence of dry grasslands sheltering more xerophilic species (*J. quadridens*). Signs of a bioclimatic

improvement appear from level 5c (whose ^{14}C dating to *c.* 11 200 cal. a BP is too young) to level 6d (12 725 to 12 625 cal. a BP). Nevertheless, the extension of the swamp prevents any more general perception of the landscape. Tufa of level 8 provides without transition a xerophilic and more thermophilic assemblage that indicates an open habitat. This change is commensurate with the strength of the detrital deposit that precedes it (level 7). The ^{14}C dating obtained for this abrupt event is not satisfactory.

MIR-5 Le Verger

Stratigraphy. – The lower part of the formation was investigated by backhoe drilling to a depth of 4 m, but its base was not reached (Fig. 2). A first sedimentary ensemble begins with tufa alternating with stony layers (levels –12 to –1b). It is dated to the LGI. A second ensemble probably starts with level 2a. Level 2b is dated to the end of the Boreal period (8760 to 8425 cal. a BP).

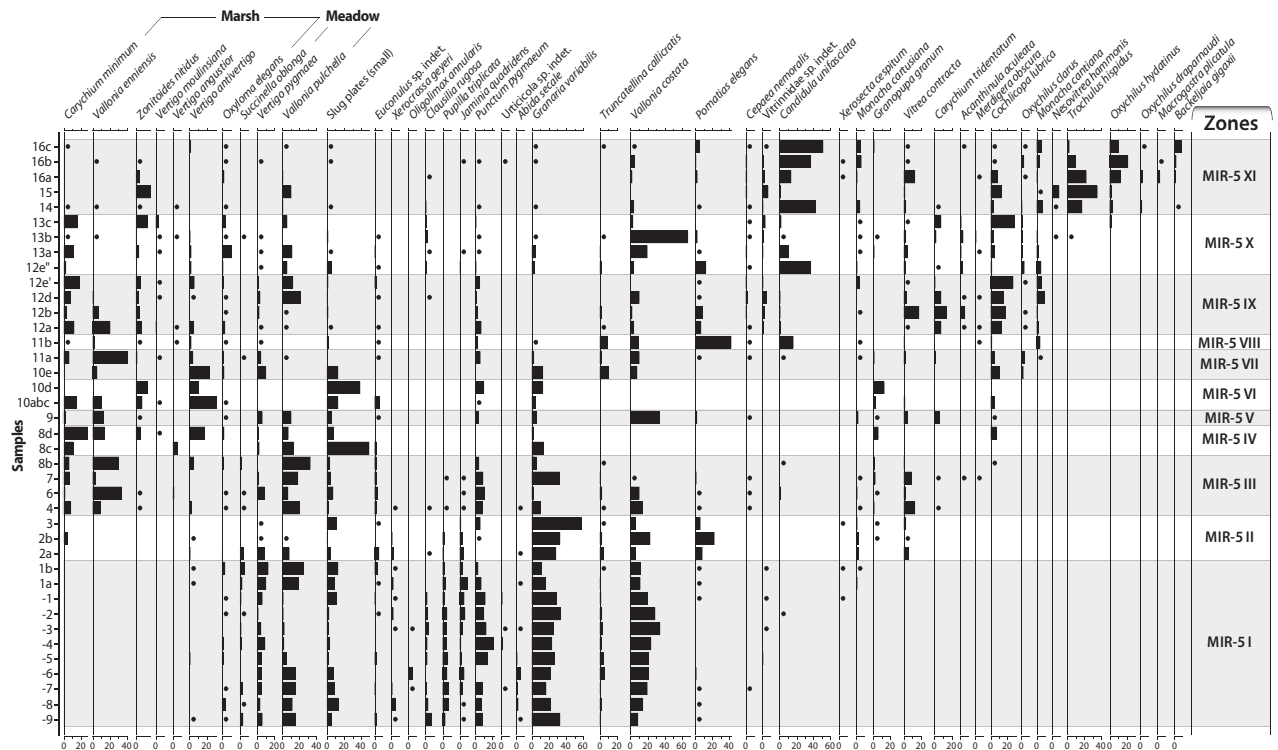


Fig. 6. Mir-5 Le Verger molluscan succession. Percentage histogram: terrestrial taxa. Dots = values less than 1%.

This layer stands out with its grey colour and pedomorphic traits. The sedimentation then changes abruptly. Chalky again, it is sometimes interrupted by hints of hydromorphic soils or coarse detrital layers (levels 3–7). From level 8a to level 11a, the sediment is chalky and detrital layers are rare. Structured tufas then develop. They alternate with chalky facies and silty detrital layers, sometimes displaying pedomorphic traits. Only radiocarbon datings reveal a major discontinuity between level 1b and level 2a or 2b, i.e. between $10\ 960 \pm 30$ and 7775 ± 65 uncal. a BP.

In the upper part of the section, levels 12b, 12d and 12e contained Late Neolithic sherds. Numerous pottery sherds, flint shards and charcoals in level 14 then testify to a Late Neolithic settlement (5421 to 4989 cal. a BP). The last level of the section (16d) includes sherds dated to Late Antiquity.

Stratigraphic distribution of mollusc assemblages. – Thirty-nine samples were analysed (Table S2; Figs 2, 5, 6, S2).

Zone MIR-5 I (assemblages –9 to 1b). The share of aquatic molluscs is extremely low. The same applies to marsh species (*V. antivertigo* and *O. elegans*). Wet meadow snails are abundant (up to 40% of assemblage 1b). The two dominant ecological groups are mesophilic species of various habitats and xerophilic species of open habitats. The first group consists of *V. costata* and *P. pygmaeum*. There is a relative consensus that

P. pygmaeum is included among the species of varied habitats (Davies & Griffiths 2005; Davies 2008), although it may be attributed to greater preferences for treed ones (Evans 1972; Magnin *et al.* 2022). The case of *V. costata* is thornier. This species is classically assigned to the open country or open ground group (Ložek 1964; Evans 1972; Puisségur 1976; Juříčková *et al.* 2014), but it can be found in open woodlands (Evans 1972; Thomas *et al.* 1982; Magnin 1991; Martin 2004; Davies & Griffiths 2005; Magnin *et al.* 2022) and even in marshes (Evans 1972; Davies 2008). It therefore must be given a greater ecological tolerance. *Granaria variabilis* predominate the second group, accompanied by *Pupilla triplacata*, *J. quadridentata* and *T. callicratis*, with also *X. geyeri*, *O. annularis* and *Urticicola sp.* *Xerocrassa geyeri* and *O. annularis* are currently more montane (Magnin 1989, 1991, 1993b). Among the species of open environments, however, we note the appearance of *Candidula unifasciata* from level –2, then more thermophilic species from level –1 (*Xerosecta cespitum* and *Monacha cartusiana*). Finally, there are rare fragments of shells and opercula of *Pomatias elegans*, a semi-forest and thermophilic snail.

Zone MIR-5 II (2a, 2b and 3). Aquatic and marsh malacofauna is almost absent and the marsh share is extremely low. Hygrophilous species and *P. pygmaeum* are poorly represented. We note the importance of dry open habitat taxa and the very relative abundance of the woodland component. The proportion of xerophilic

open ground molluscs is steadily increasing by 44–65%, mainly thanks to *G. variabilis* which is accompanied by species present from the Lateglacial (*X. geyeri*, *P. triplicata*, *J. quadridens* and *T. callicratis*) and more thermophilic species sometimes reported in the latest assemblages of zone MIR-5 I (*X. cespitum*, *M. cartusiana*, *Granopupa granum*). The woodland-dwelling malacofauna is not diverse. With *P. elegans* (200 shells in 2b), we can find *Vitrea contracta* (mesophilic species sometimes considered to be woodland; Evans 1972) and *V. costata*, which appears to be promoted in this case by the development of an open woodland.

Zone MIR-5 III (4–8b). A marsh is established from assemblage 4. It will reach its maximum in zone MIR-5 VI, with a switchback trend, before regressing. In MIR-5 III, the aquatic component increases from 5 to 22%. It is mainly the amphibious snail *G. truncatula*. Marsh malacofauna fluctuates between 10 and 34%, with *C. minimum*, *V. enniensis* and *V. antivertigo*. *Vallonia pulchella*, a damp meadow species, accounts for up to one-third of the malacofauna. The dry open ground and woodland components are reduced. Dry open-ground species (*G. variabilis*) have low values, except for sample 7, which shows a brief retraction of the marsh. Woodland snails are anecdotal but, for the first time, strictly woodland species occur (*Acanthinula aculeata* and *Merdigera obscura*). *Punctum pygmaeum*, *V. contracta* and *V. costata* may be added to this woodland component. The persistence of the last specimens of *X. geyeri*, *P. triplicata* and *A. secale*, three species among the most characteristic of Lateglacial assemblages, is noticeable.

Zone MIR-5 IV (8c and 8d). This zone is characterized by a decrease in abundance and species richness, and a preponderance of marshland snails. In 8c, the small-sized slug plates make up 50% of an impoverished assemblage. In 8d, the aquatic (*G. truncatula*), marsh (*V. enniensis*, *C. minimum* and *V. antivertigo*) and hygrophilous (*C. lubrica*) species predominate. In this zone and the previous one, the marsh in which the tufa formed is the most visible environment. *Phragmites* sp. indet. is abundant within charcoal assemblages (Beauvais & Cazorla in Martin 2004). This kind of *Phragmites* meadow acts as a filter so that it is no longer possible to perceive the landscape around the wetland.

Zone MIR-5 V (9). This zone shows the expansion of *V. costata* and a brief decline in aquatic and marsh components, *V. enniensis* excepted.

Zone MIR-5 VI (10abc and 10d). The marsh component reaches its maximum before a final switchback regression. Zone MIR-5 VI is roughly the same as the pattern of

zone MIR-5 III. However, the composition of the marsh fauna is changing slightly. *Carychium minimum* and *V. enniensis* are downgraded to the benefit of *Z. nitidus* and *V. antivertig.* Meadow species *V. pulchella* is dropping dramatically. The proportion of molluscs from dry open ground is low (*G. granum* and *G. variabilis*). Forest dwelling species are absent.

Zone MIR-5 VII (10e and 11a). The aquatic malacofauna is more diverse, with three stygobionts species, molluscs of temporary waters (*G. truncatula*) and more demanding species (*Radix balthica*, *Ancylus fluviatilis*). There is a peak in the marsh species *V. enniensis* and the return of meadow species (*V. pygmaea*, *V. pulchella*). *Truncatellina callicratis* is among the dry open ground snails. For the first time, the presence of *Oxychilus clarus* (very abundant) and *M. cantiana* is observed as potentially woodland species. On the other hand, there are only three shells of *P. elegans* in 11a.

Zone MIR-5 VIII (11b). The swamp had begun to withdraw as early as zone MIR-5 VI, but there is now a short-lived but particularly marked decline in aquatic, marsh and hygrophilous molluscs. Assemblage 11b is dominated by *P. elegans* (685 shells) and *C. unifasciata* (261 shells), which are accompanied by *V. costata*, *T. callicratis* and *M. cantiana*. Stenotopic woodland species are almost absent (two *M. obscura* shells). This kind of assemblage is currently characteristic of open and immature downy oak stands developed on loose and deep soils. *Granaria variabilis* definitively loses the place it has occupied since the Lateglacial.

Zone MIR-5 IX (12a–12e'). After a short recovery, the swamp resumes its gradual decline. Among aquatic species, only stygobionts remain well represented, especially *Fissuria boui*. Their presence is linked to the karstic source. The retraction of the marsh temporarily benefits *V. pulchella* (wet meadow) and *C. lubrica* (hygrophilous, varied habitats). *Pomatias elegans* is present but without the overabundant numbers it had in zone MIR-5 V. It is still accompanied by *V. costata* and *M. cantiana*, but the strictly forest species are now better represented (*A. aculeata*, *M. obscura*, *Lauria cylindracea*). *Carychium tridentatum* and *O. clarus* can be added to this pool despite their larger tolerance.

Zone MIR-5 X (12''–13c). The local environment is unstable, and three phases can be distinguished. The first is Phase a, a peak in dry open ground taxa, particularly *C. unifasciata* (37% in 12'') with *V. costata* and *G. variabilis*. Dry herbaceous habitats are therefore expanding significantly in a heterogeneous landscape. This opening may be connected to a nearby Neolithic settlement revealed by a few sherds in levels 12c and 12d. The second is Phase b – in assemblage 13b, the number of *V. costata* is

impressive (67% of the assemblage). It is likely that this species of varied habitats benefits from the presence of tree cover. Among the woodland species *sensu lato*, *P. elegans* does not reach the overabundance observed in zones MIR-5 II and MIR-5 V. It is quite abundant, however, and it is accompanied by notable populations of *A. aculeata* and *M. obscura*. Added to this trio is a group of snails often living in woodland habitats: *C. rugosa*, *V. contracta*, *C. tridentatum*, *O. clarus*, *M. cantiana* and *Nesovitrea hammonis* (first occurrence). The malacofauna of dry open habitats is represented almost only by a few *C. unifasciata*. A marshy biotope is still present, although limited (*Z. nitidus*, *V. antivertigo* and *C. minimum*). Such an assemblage could characterize a fairly closed riparian forest. Third is Phase c – finally, assemblage 13c shows a new incursion of a marshy grassland (*Z. nitidus*, *C. minimum*, *O. elegans*, *V. pulchella*) and a withdrawal or displacement of the riparian woodland.

Zone MIR-5 XI (14–16c). This last zone shows a strong retraction of wetlands species despite their brief return in level 15. Species of dry open environments are rising strongly (28–79% of the malacofauna, except for assemblage 15). The opening up of vegetation is evident with *C. unifasciata* whose progression from zone MIR-5 VIII reaches its maximum here. The development of a dry grassland also promotes *M. cartusiana*, *Oxychilus hydatinus* and *B. gigaxii*. The rise of *Trochulus hispidus*, which appeared on the site a little earlier, denotes the maintenance of a certain humidity culminating in level 15. In addition to *O. hydatinus*, which was introduced to the region during the Neolithic Period, and *T. hispidus*, whose populations in Provence seem to be recent, we note the arrival of *Oxychilus draparnaudi* (synanthropic), but also of humid woodland taxa such as *Helicodonta obvoluta* and *M. plicatula*. There is a mosaic dominated by dry open habitats, with a turnover that involves three ecological groups: the dry open ground species, the species of various habitats and the woodland species.

Sketch of environmental changes at Le Mirail MIR-5 Le Verger. – Zone MIR-5 I, at the base of the succession, corresponds to a part of the LGI, between 13 589 to 13 346 cal. a BP (level –9) and 12 983 to 12 770 cal. a BP (level 1b). The malacofauna suggests the juxtaposition of a sparsely swampy meadow and a dry grassland or scrubland. Apart from wet meadow species, these assemblages could be found today in supra-Mediterranean open habitats. Thermophilic species appear to develop from assemblage –1 dated at 13289 to 13094 cal. a BP. After a hiatus revealed by the ¹⁴C dating of level 2b (8760 to 8425 cal. a BP), zone MIR-5 II indicates an open and dry woodland. Charcoals (Beauvais & Cazorla *in* Martin 2004) belong to *Quercus* sp. (deciduous) with heliophile and thermophilic species

such as *Rosmarinus*. The tufa then forms in a temporarily flooded *Phragmites* meadow (zone MIR-5 III). The last species remaining from the Lateglacial disappear here. At the same time, we note the presence of the first stenotopic woodland snails. The preponderance of wetlands increases further in zone MIR-5 IV (7592 to 7275 cal. a BP) before a brief shortening (MIR-5 V). It is in zone MIR-5 VI that the marsh malacofauna reaches its maximum. At that time, we faintly perceive the existence of dry open habitats nearby. Woodlands are undetectable. Zone MIR-5 VII (5577 to 5331 cal. a BP) marks a change in the marsh dynamics. The malacofauna is diversifying and includes more species, suggesting concentrated flows. A riparian forest is developing. The swamp then reduces abruptly (zone MIR-5 VIII), and an open and immature woodland develops, associated with dry herbaceous vegetation. During zone MIR-5 IX, the swamp continues its gradual retreat after a short-lived return. A woodland is maintained next to a marshy meadow. It is more mature than that of the previous zone. We then observe (zone MIR-5 X) a succession including an opening of the woodland, then the return of a riparian forest, and finally the last substantial spread of the swamp. At the top of the section, zone MIR-5 XI shows the definitive reduction of the marsh, a considerable increase in open habitats and a taxonomic turnover, the latter two phenomena being certainly attributable to human activities. Level 14 corresponds to a Late Neolithic settlement dated at 5421 to 4989 cal. a BP, while ceramic shards from Late Antiquity are found in the upper levels (16b, 16c).

La Thomassine, Manosque

Stratigraphy. – The deposit begins with a remnant of pseudogleyed sandy silts (S1 level; Fig. 2). It is followed by a set of greyish brown silts containing charcoal and heated pebbles. There are three layers in this set. The first layer (S2; 8362 to 8196 cal. a BP) contains calcareous gravels and some *C. nemoralis* shells. The second layer (S3), more clayey, contains numerous shells of *P. elegans*. These shells are less abundant in the third layer (S4) at the top of which some tufa begins to appear. We can then observe an alternation of compact tufa with plant imprints (levels 1 and 4) and softer, chalky sediments with a few tufa concretions (levels 2 and 3, c.7500 to 7400 cal. a BP). After a rapid transition through a terrigenous tufa (level 5a0), a detrital event interrupts the development of the tufa. It begins with a stony deposit (5a), continues with massive yellow silts (5b; 6834 to 6671 cal. a BP), then with massive grey silts rich in charcoal (6). The next level (7) is a structured tufa with plant imprints, containing chalky inclusions (7a) and a stony layer (7b). The sedimentary succession ends with a terrigenous tufa (8; 4854 to 4656 cal. a BP).

Discreet evidence of human activity has been found at three spots in the stratigraphy. In the S2 level (Late

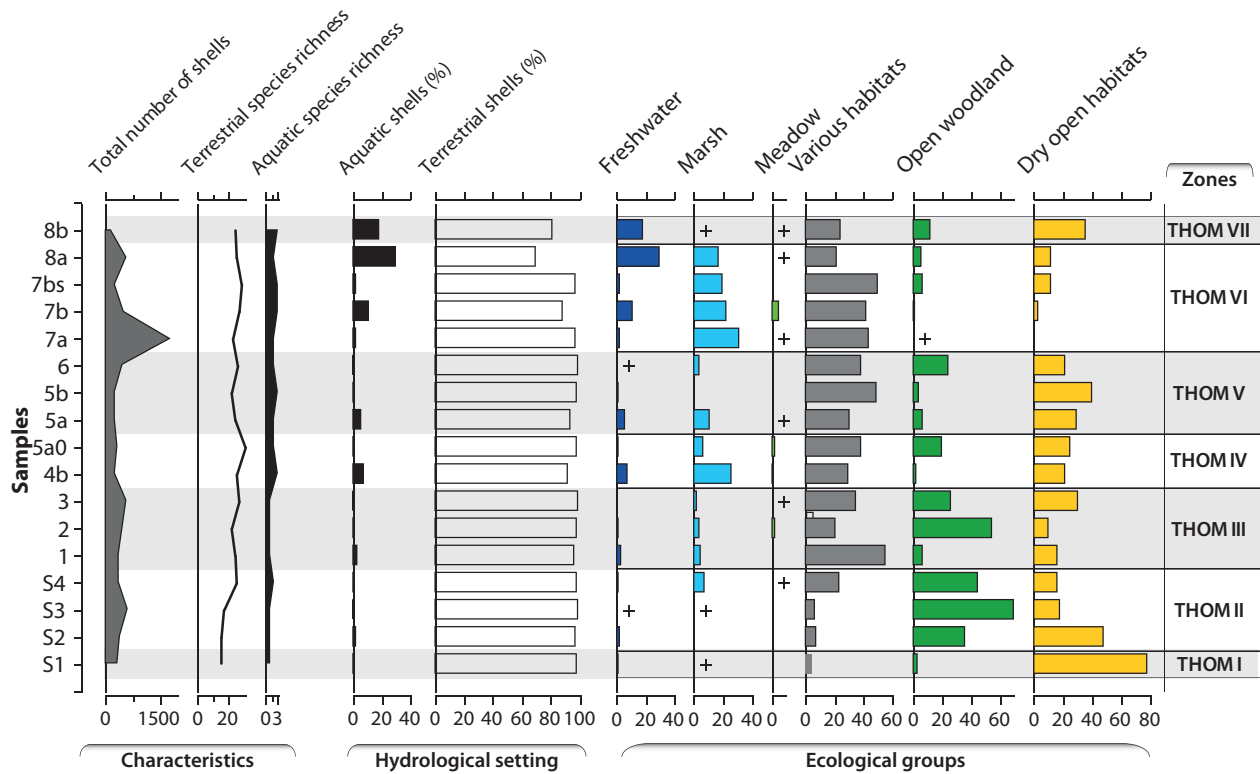


Fig. 7. La Thomassine molluscan succession. Assemblage characteristics and ecological groups. Plus signs = values less than 1%.

Mesolithic) it is a combination of charcoal, charred fruit fragments and heated stones. A single pottery fragment was then found in level 5a while levels 5b and 6 yielded splinters of burnt bones, heated pebbles, very fresh flint shards, numerous charcoal fragments and rare charred cereal seeds (*Hordeum vulgare* var. *nudum*). These levels correspond to an Early-Middle Neolithic settlement in the neighbourhood. Finally, level 8b gave up charred cereal seeds (*Hordeum vulgare*) as well as flint shards and fragments of rammed earth and pottery that come from a settlement of the Late Neolithic.

Stratigraphic distribution of molluscs. – Seventeen samples were taken (Figs 2, 7, 8, S3; Table S3).

Zone THOM I (assemblage S1). The open ground species *G. variabilis* and *J. quadridens* predominate. Other species in this group are *X. geyeri* and *G. granum*, along with rare *X. cespitum* and *B. gigaxii*. That is 80% of the assemblage. There is also a share of mesophilic and woodland species such as *C. nemoralis*, *O. clarus*, *P. pygmaeum*, *P. elegans*, *A. aculeata* and *M. obscura*. It is questionable whether at least some of these rare woodland species do not belong to the upper layers, in the same way as the dated charcoal fragments. It is an assemblage of dry grassland, with some trees. *Xerocrassa geyeri* is a Lateglacial relic that will be present in small numbers as far as zone THOM VI. If the shells of *X.*

cespitum, *B. gigaxii* and *P. elegans* were in place, their presence would argue in favour of a dry but not cold climate.

Zone THOM II (S2, S3 and S4). There is a gradual decline of open ground species in favour of *P. elegans* whose shells form a concentration in level S3 (422 shells). There are *C. nemoralis*, a few *A. aculeata* and large slug plates. However, open-habitat species remain well represented (17–48%). *Oxychilus clarus* is developing. Marsh (*O. elegans*, *Z. nitidus*, *C. minimum* and *V. antivertigo*) and hygrophilous molluscs (*V. pygmaea*, *Euconulus* sp., *P. pygmaeum*, *C. lubrica* and *C. tridentatum*) begin to develop at the end of this zone, at the same time as the tufa. This is an open woodland that remains dry until S4.

Zone THOM III (1, 2 and 3). *Galba truncatula* accompanies the development of marsh and hygrophilous species (*O. elegans*, *V. pulchella*, *C. lubrica* and *C. tridentatum*). Mesophilic snails are also more abundant (*O. clarus*, *P. pygmaeum* and *Vitrinidae* sp. indet.); they often have woodland preferences. The numbers of *P. elegans* are high, with also many *A. aculeata*, a stenotopic woodland species. *Monacha cantiana* is present. This snail is currently common with *P. elegans* in open woodlands. The proportion of dry open ground snails is still 10–30% (*G. variabilis*, *T. callicratis* and *M.*

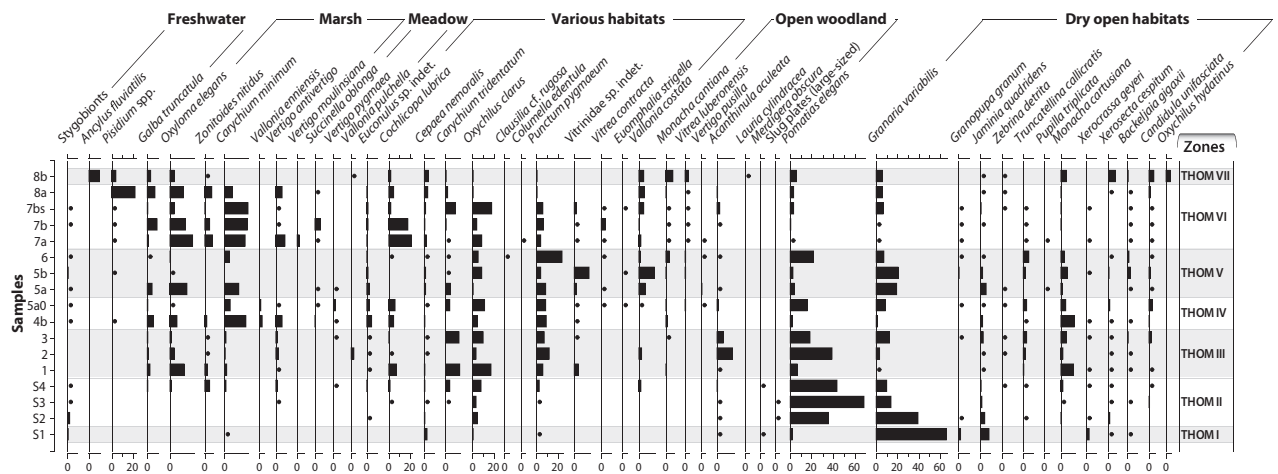


Fig. 8. La Thomassine molluscan succession. Percentage histogram. Dots = values less than 1%.

cartusiana) but *M. cartusiana*, occasionally hygrophilous, could indicate here the development of a *Phragmites* meadow. There is a change in the nature of the woodland, which would be a riparian forest. This evolution began as early as S4, at the end of THOM II.

Zone THOM IV (4b and 5a0). In a first step (4b), the marsh malacofauna increases (*G. truncatula*, *C. minimum*, *V. enniensis* and *V. antivertigo*) as well as the hygrophilous component sensu lato (*Euconulus* sp., *S. oblonga* and *V. pygmaea*). *Monacha cartusiana* seems to be related to this change and the existence of a *Phragmites* meadow. In a second phase the marsh malacofauna declines, unlike the species that can be linked to the riparian woodland (*P. elegans*, *A. aculeata*, *M. cantiana*, *V. contracta*, *O. clarus* and *C. tridentatum*). *Vitrea contracta*, *V. luberonensis* and *V. pusilla* occur at the site for the first time. Dry open-ground molluscs still account for 10–20% of the malacofauna (excluding *M. cartusiana* because of its ambivalent meaning). There is a mosaic of environments including a moist meadow, a riparian woodland and drier open habitats, components that move spatially or whose proportions vary over time.

Zone THOM V (5a–6). The proportion of dry open ground snails is increasing (40% of assemblage 5b; *G. variabilis*, *J. quadridens*, *T. callicratis*, *B. gigaxii* and *C. unifasciata*). The meaning of *M. cartusiana* is still ambivalent. Woodland snails are declining, but there is a renewal in assemblage 6 with *P. elegans* and *M. cantiana*. Actual forest species are accidental (*A. aculeata*, *V. pusilla* and *V. luberonensis*). Mesophilic species and species from various habitats are well represented: *O. clarus*, *P. pygmaeum*, *Vitrinidae* sp. indet. and *V. costata*. There is a drop in the abundance and

richness of wetland molluscs. The opening of woodland is significant in this zone, which also corresponds to a withdrawal of the marsh. A slight woodland recovery is noticeable in level 6.

Zone THOM VI (7a–8a). The aquatic and marsh fauna reach its maximum. Aquatic molluscs culminate in assemblage 8a (*Pisidium* spp. and *G. truncatula*). They still characterize temporary waters. Marsh snails account for one-third of the malacofauna in assemblage 7a and this proportion decreases to assemblage 8a (17%). These are *O. elegans*, *Z. nitidus*, *C. minimum*, *V. antivertigo* and *V. moulinsiana*. The peak of *C. lubrica* (7a, 7b) is related to the marsh context. Species with forest preferences are declining, including *P. elegans*. However, *A. aculeata* and mesophilic species such as *O. clarus* and *P. pygmaeum* persist. They may indicate the presence of a riparian woodland. Dry open-habitat species are also regressing, especially in levels 7a and 7b. *Granaria variabilis* remains the dominant species in this group along with *C. unifasciata* and *J. quadridens*. This zone is characterized by the importance of the marsh, the surrounding environment being hardly visible. As for level 8a, there is at the same time a reinforcement of the aquatic functioning and a decrease in ambient moisture around the stream.

Zone THOM VII (8b). There are almost no marsh species, except *O. elegans* which lives at the water edges. A species of running water (*Ancylus fluviatilis*) was found for the first time. Hygrophilous species are rare, as well as species with woodland preferences (*P. elegans*). It is the dry open-habitat component that is on the rise: *M. cartusiana*, *C. unifasciata*, *X. cespitum* and *O. hydatinus*, the latter species having been introduced to the region during the Neolithic (Magnin *et al.* 2022). Flows are now concentrated within a drier, more open environment.

Table 2. Composition of the Lateglacial malacofauna from Vallon du Mirail (MIR-1 and MIR-5). Species frequency in the loess of the Durance valley: (*) = rare; * = present; ** = common or very common (according to Granier 1976).

Main type of species/environment relationship	Species		
I. Eurythermal species from dry open-ground environments (grasslands, scrublands, steppe)	<i>Xerocrassa geyseri</i> **	<i>Urticicola</i> sp.*	
	(Small slug plates*)	<i>Clausilia rugosa</i> *	
	<i>Jamina quadridens</i> *	<i>Truncatellina callicratis</i> *	
	<i>Vertigo pygmaea</i> (*)	<i>Abida secale</i> *	
	<i>Punctum pygmaeum</i> *	<i>Vallonia costata</i> **	
	<i>Granaria variabilis</i> **	<i>Pyramidula pusilla</i>	
	cf. <i>Vitrina pellucida</i>	<i>Oligolimax annularis</i> *	
	<i>Pupilla triplicata</i> **	<i>Pupilla muscorum</i> *	
	<i>Oxyloma elegans</i>	<i>Cochlicopa lubrica</i> (*)	
	<i>Succinella oblonga</i> (*)	<i>Zonitoides nitidus</i>	
II. Palustrine, eurychoric species. Azonal, marsh environment	<i>Eucomulus alderifulyvus</i> *	<i>Vertigo moulinsiana</i>	
	<i>Vallonia pulchella</i> (*)	<i>Carychium tridentatum</i>	
	<i>Galba truncatula</i> (*)	<i>Carychium minimum</i>	
	<i>Vertigo antivertigo</i>	<i>Cepaea nemoralis</i>	
	<i>Vallonia enniensis</i>		
	<i>Pomatias elegans</i>	<i>Candidula unifasciata</i> *	
	<i>Xerosecta cespitum</i>	<i>Baceljaia gigaxii</i>	
	<i>Monacha cartusiana</i>		
	III. Temperate species, even Mediterranean. Mainly open-ground environments		

Sketch of environmental changes at La Thomassine. – At the base of the section (THOM I; S1), the dominant species reflect a steppe and a temperate climate. A hiatus possibly separates this thin sedimentary remnant from the next layer. An age of *c.* 9000 cal. a BP is conceivable given what has been described in the Aix-en-Provence region (Magnin *et al.* 2022). The brown silts of zone THOM II were deposited in a dry open woodland. At their base (S2), a radiocarbon measurement indicates the end of the Mesolithic (8365 to 8193 cal. a BP). The presence of charcoal, charred fruit fragments and heated pebbles suggests an anthropogenic impact. The context becomes wetter in the S4 level which contains the first signs of the tufa formation that will follow. The first tufa (level 1) is dated to the very end of the Mesolithic or the very beginning of the Early Neolithic (8362 to 8196 cal. a BP). Its appearance may simply be a consequence of a lateral migration of the stream. The increase in local humidity leads to a change in vegetation that now resembles a riparian forest associated with a *Phragmites* meadow (THOM III; levels 1–3). This tufa and associated sediments were deposited very quickly, as shown by the similar dates obtained in levels 1 and 3, *c.* 7450 cal. a BP. During zone THOM IV, the vertical and lateral variations of facies are related to the evolution of a mosaic comprising a *Phragmites* meadow, a riparian forest and drier open biotopes. Zone THOM V then marks a radical change in sedimentation and the environment. A detrital deposit is set up in a context of decline of the swamp and of woodland, while dry open environments expand. Nevertheless, an open woodland is soon reconstituted (level 6). Artefacts and other indices in levels 5a–6 indicate a nearby settlement during the Early-Middle Neolithic (6834 to 6671 cal. a BP). There is then a tufa with plant imprints, which develops in a *Phragmites*-type meadow, possibly together with

a riparian woodland (THOM VI; levels 7a–8a). The formation of this important tufa in the sequence begins *c.* 6674 to 6496 cal. a BP and continues beyond 6445 to 6309 cal. a BP. The last zone (THOM VII; level 8b) is characterized by a concentration of running water in an overall drier and more open landscape. Small fragments of rammed earth and pottery as well as charred cereal seeds indicate a settlement of the Late Neolithic (4854 to 4656 cal. a BP).

Discussion

The Lateglacial snail communities and their environmental significance

Lateglacial deposits are particularly thick in the Mirail valley. Mostly carbonated, including stony layers, they correspond for the most part to the LGI. The two earliest dates would place the base of the MIR-1 succession at the end of the Oldest Dryas. The top of this same succession is probably attributable to the Younger Dryas. The Lateglacial terrestrial malacofauna is rich with 33 taxa to which we can add the amphibious species *G. truncatula*. These taxa can be split into three main clusters (Table 2).

Cluster I is more or less the malacofauna of the loess-like silts ascribed to the Würmian Pleniglacial in the south of the Rhone valley and western Provence (Mazenot 1956; Bourdier 1961; Bonifay 1962; Granier 1976; Magnin 1989, 2014). It is characterized by its low species richness and its homogeneity, except for slight intra-regional variations. It is more xerophilic and, at first glance, more temperate than that of the more northerly loess (Mazenot 1956; Granier 1976; Magnin 1989). As in the north (Limondin-Lozouet & Antoine 2001), the LGM malacofauna of SE France

has suffered a dramatic impoverishment. It has spared only a small number of xerophilic and climate-tolerant species which today have a wide altitudinal distribution. Only two species (*O. annularis* and *X. geyeri*) are nowadays confined to montane refuges. Changes in their geographical distribution, nevertheless, are not a strict and unequivocal response to climate variations (Magnin 1991, 1993a, b). In short, the basis of the Lateglacial malacofauna of the Luberon is a direct legacy of the LGM malacofauna, with a better representation of less xerophilic species that were previously characteristic of the mid-Rhone valley.

Cluster II includes hygrophilic, marsh and amphibious species. It is a substantial group that contains only common species with a wide geographical distribution. Such a component is not determined solely and directly by climate. Local factors can play a significant role. Therefore, it is not easy to distinguish between local factors and climatic fluctuations to explain the increase of wetland species.

Cluster III includes taxa that are rather cold sensitive. More than half of them are of Mediterranean origin. *Candidula unifasciata* is an exception as it reaches about 2300 m a.s.l. in the Alps (Magnin 1991; Boschi 2011). The other species in this group are thermophilous (*X. cespitum*, *P. elegans*, *M. cartusiana* and *B. gigaxii*). However, except for *P. elegans*, the case of which will be discussed later, these taxa occur only in the most recent Lateglacial levels of MIR-5, near the major unconformity brought to light in the stratigraphy. Being scarce and often poorly preserved, these shells are probably intrusive Holocene elements. While some succession in Basse-Provence seem to corroborate such Lateglacial ages for several of these species (Magnin *et al.* 2022), other data would indicate a later development, between 11 500 and 10 000 cal. a BP (Magnin, in prep.).

The growth of the hygrophilic and marsh components (cluster II) is the most distinctive feature of the Lateglacial malacofauna here studied. It probably arises from LGM wetlands, which were certainly very localized, for there are no examples of marsh malacofauna attributable to this period in the region. These hygrophilous species are primarily an indicator of the local moisture budget. Interpreting the gradations observed within the Lateglacial malacofauna in terms of climate and vegetation structure is challenging (Fig. 9).

Oldest Dryas and Oldest Dryas/LGI transition. – The assemblages of at least the first two zones of the MIR-1 succession, with low species richness, including *X. geyeri*, *C. rugosa* and *A. secale*, resemble those of the Pleniglacial loess. Only the presence of hygrophilous species *sensu lato* distinguishes them from the communities that nowadays live on the ridges of Mont Ventoux or Montagne de Lure ~1800–1900 m a.s.l., in dry grasslands and scrublands with stunted *Juniperus* and *Pinus* (Magnin 1989, 1991). Although no strict indicator

species can be found, the climate was possibly cold but less arid than during the LGM. The dates obtained on levels 2 and 3d of MIR-1 would place the two malacological zones MIR-1 I and MIR-1 II – or even the beginning of zone MIR-1 III – at the end of the Oldest Dryas. Zone MIR-1 III appears to be a transition, the real change in malacofauna being placed at level 5a. Sedimentary signs of warming related to the LGI – such as pedomorphic traits and the onset of calcareous tufa, as early as level 3a – would therefore precede both the accepted age for the beginning of the LGI (i.e. 14 700 cal. a BP) and changes in malacofauna. In the French Massif Central, Ponel *et al.* (2016) present two examples in which an increase in lacustrine productivity and an expansion of *Juniperus* and *Salix* predate the age of 14 700 cal. a BP. We may have the same situation here. As for the changes in malacofauna in our case, it would not be surprising if they occurred with a delay compared with vegetation and the shift in morpho-sedimentary dynamics. Unfortunately, there is a lack of dating in the middle part of MIR-1 section, especially within zone MIR-1 III.

Allerød. – This is first marked, during zone MIR-1 III, by an increase in species richness. This increase benefits on the one hand a set of rather xerophilic species of open environments, and on the other hand the palustrine and hygrophilous species whose number varies according to local conditions. A small number of species from various habitats also contribute to this enrichment. The malacofauna of northern France similarly shows an increase in species richness, but a shift towards drier conditions, although with regional nuances (Limondin-Lozouet & Antoine 2001). This general trend towards more drought is less evident in the south. Up to 12 700 cal. a BP, the malacofauna is globally richer in hygrophilous taxa than that of the Pleniglacial loess. This assumes at least a high moisture budget and probably more precipitation. However, the variations within the LGI may only have a local basis depending on the hydro-geomorphological context. This is possibly the case for the marsh event MIR-1 IV, which is not found in the MIR-5 succession located further upstream. Several pollen records support the evidence of a general north to south climatic gradient showing a climate steadiness or warming in southern Europe during the Allerød (Combourieu-Nebout *et al.* 2009; Ponel *et al.* 2016). The arrival here and good representation of a snail like *J. quadridens* could be a weak sign of a less severe climate. Such an interpretation has been proposed for older assemblages in Provence that would correspond to climate improvements during MIS 3 (Magnin 1991, 1992, 2014). Nowadays this species is relatively thermophilic (Germain 1930) but there are notable exceptions in the Alps where it can reach 2400 m a.s.l. (Aubry 2003; Boschi 2011). An interpretation of the malacofauna in terms of temperature therefore remains complex. There is little contrast in the observed changes, not necessarily because climate did

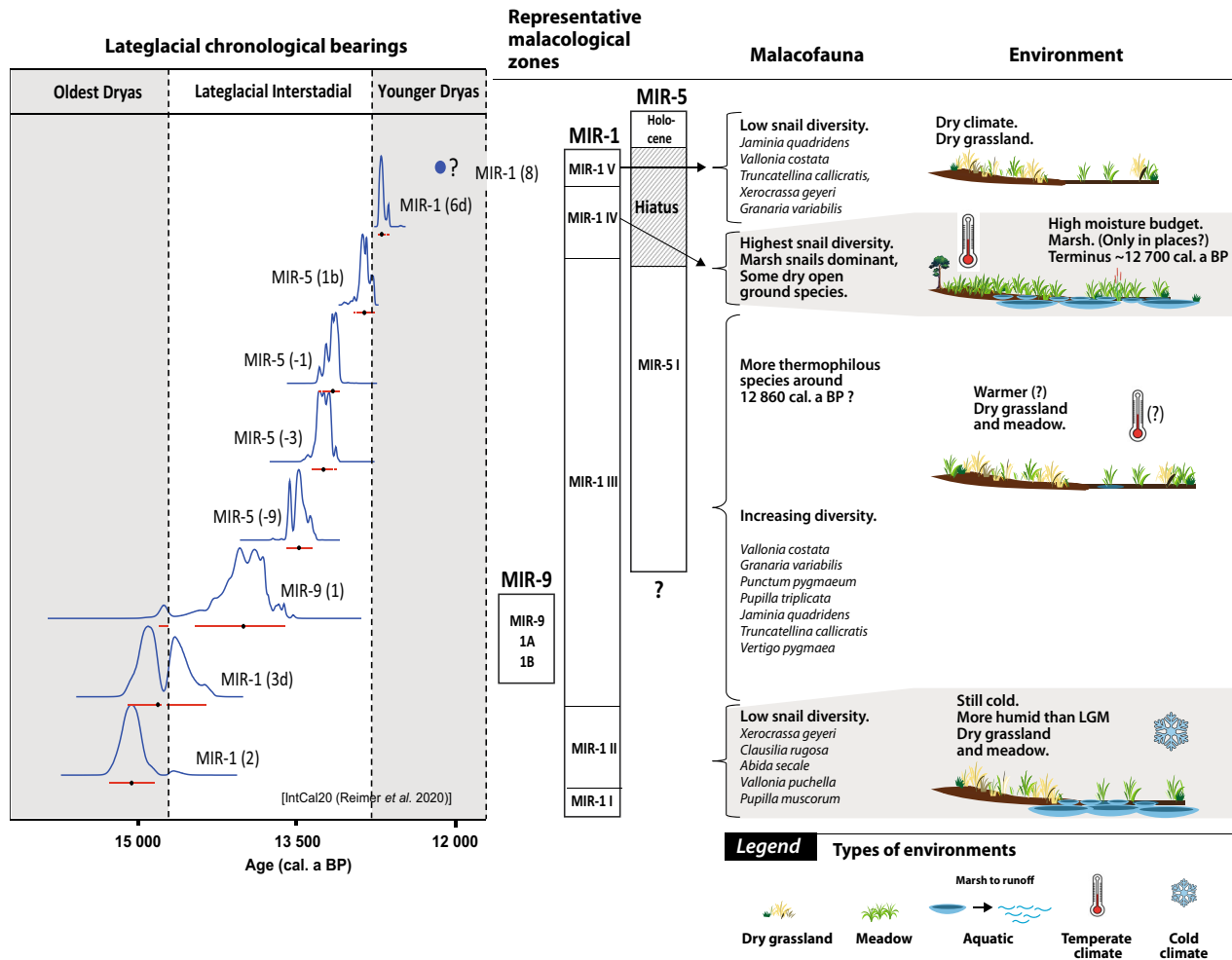


Fig. 9. Summary of the Lateglacial molluscan succession on the southern slope of the Luberon mountain range (MIR-9 according to Ollivier (2006) and unpublished data).

not change, but potentially, following the LGM, because of the reduced pool of species both available and in equilibrium with the new environment. Almost all taxa locally available for recolonization during the LGI are climate tolerant. Moreover, the diversity of distributions nowadays observed, from one mountain range to another, highlights the multiplicity and complexity of the drivers of these distributions, which are not restricted to climatic factors (Magnin 1991, 1993a; Aubry 2003; Aubry *et al.* 2005).

In the western Mediterranean area, according to some authors, the LGI would correspond to the development of a deciduous oak forest, with Mediterranean taxa, at the expense of steppe vegetation (Pons & Reille 1988; Combourieu-Nebout *et al.* 2009; Delhon *et al.* 2010; Ermolli *et al.* 2022). Only 50 km SE of the Luberon, the Allerød seems to be characterized by the juxtaposition of several types of vegetation: a riparian forest around the pollen site, a pioneer vegetation with *Pinus* and *Juniperus*, and a mesophilic vegetation including *Quer-*

cus, while steppe taxa remain abundant (Nicol-Pichard 1987). Towards the Rhone Valley, in a less sheltered area, this steppe character remains very pronounced (Triat-Laval 1978). Regarding Mediterranean France in general, Beaulieu *et al.* (2005) describe the dominant landscape of the LGI as a wooded steppe with abundant *Juniperus* and *Pinus* and only scattered stands of deciduous oaks. In our study of the Luberon, the malacofauna seems to show that the vegetation cover stayed steppe-like during the entire LGI. No forest species have been added and the species regarded as semi-forest, always accidental, are either potentially assignable to other ecological categories (*C. nemoralis*) or of doubtful origin as is the case with *P. elegans*, the most common and least demanding woodland-dwelling species in Mediterranean France (Pfenninger 2002). Only a very few residual *P. elegans* shells were recovered from the Lateglacial deposits of sections MIR-1 and MIR-5. These are probably reworked. Indeed, in another section of the Luberon dated on charcoal *c.* 12 000 uncal. a BP,

this kind of fragment gave a ^{14}C measurement of $43\,100 \pm 730$ uncal. a BP, much too old to be attributed to a limestone effect (Magnin, unpublished data). Biases that may be related to the presence of residual, worn nepionic shells of *P. elegans* are common (Evans 1972; Carter 1990).

As in England or northern France (Preece & Bridgland 1998; Limondin-Lozouet & Antoine 2001), the climatic improvement of the LGI has not led to any development of woodland snail communities in SE France. This could be due to the distance from refugia and the resultant delay in colonization. The problem is whether the late-glacial malacofauna that we describe strictly contradicts the existence of the forest reconquest described by several authors, or whether it may be transient, disequilibrium communities that can tolerate a certain tree cover. Almost all taxa that make up the basis of the Lateglacial malacofauna are usually classified in open country groups with the exception of several species which belong to the mesic or various habitats group, suggesting that they may be found in woodlands or at least tolerate lightly wooded habitats (Ložek 1964; Puisségur 1976; Juříčková *et al.* 2014). Near the sections here studied (Mont Ventoux and Luberon; Magnin 1991; Labaune & Magnin 2001, 2002), *P. pygmaeum* would be a shade-loving species showing a preference for woodlands and a tree cover greater than 25%. *Abida secale* and *C. rugosa* tend to have a clear preference for low tree cover (<10%), although they may live in more closed habitats. Several species classified in the open country group, including *P. triplicata* and *V. costata*, occasionally colonize more closed habitats (Magnin 1991; Magnin *et al.* 2022). Even *X. geyeri*, *Pyramidula pusilla*, *G. variabilis* and *O. annularis* can tolerate a tree cover up to 40% at most. Only *J. quadridens* (and presumably *P. muscorum*, which has not been studied) would not tolerate a tree cover of more than 10% (Magnin 1991). Such adaptability, even at a regional scale, is important to highlight. It shows that the classification in ecological groups of species considered as stenotopic should not obscure their potential plasticity that particular environmental contexts may reveal.

Finally, a strong regional heterogeneity must be considered. In the Pleistocene site of Pont-de-Mirabeau, less than 20 km SE of the Mirail valley, on a north-facing slope, malacological assemblages first attributed to the LGM on the basis of their composition and stratigraphic position (Magnin 1991, 1992) were definitively dated to the Allerød (13 039 to 13 617 cal. a BP, Ollivier *et al.* 2014). Dubar (1983) already noted that the loess malacofauna in the Durance valley varies according to the local geomorphology and topography, which can affect local climate and environment. Magnin (2014) concluded that the physiographic diversity of the region during the LGM prevents the possibility of a reliable biozonation, inter-site variability being possibly greater than intra-site. Such a phenomenon may be valid for the LGI.

Younger Dryas. – Probably referable to the Younger Dryas, zone MIR-1 V, which follows (or includes) a torrential event, reflects a rapid and severe aridification that could be due to a drastic decrease in precipitation. This evolution towards aridity agrees with regional pollen data (Nicol-Pichard 1987). Unlike what has been observed in northern France or in Britain (Preece & Bridgland 1998; Limondin-Lozouet & Antoine 2001), there is no indication of a cooling.

The laborious and incomplete reassembly of Holocene woodland communities

Early Holocene. – At the beginning of La Thomassine succession, the steppe malacofauna of THOM I may be weakly polluted by more recent forest-dwelling species. Otherwise, such an assemblage is compatible with those described at Aix-en-Provence *c.* 9000 cal. a BP, which would indicate a wooded grassland (Magnin *et al.* 2022).

Apart from this poorly dated assemblage, which could correspond to a primary stage of woodland recolonization, the first Holocene assemblages appear to be already established woodland assemblages (2a and 2b for MIR-5 and S2 for La Thomassine). The oldest are those from zone MIR-5 II (*c.* 8550 cal. a BP) (Fig. 10). Compared to the rest of the MIR-5 succession, they are characterized by their xerophilic nature, by the importance of molluscs of open habitats, and by the development of only two or three species that prefer a woodland cover. Among these species, the importance of *P. elegans* is remarkable. The conditions must have been particularly favourable for its development, with a moderately moist, loose soil and an aerated foliaceous litter. These same conditions may have promoted *V. contracta* and *V. costata*, which live in a variety of habitats and are not regularly woodland-dwelling species. In short, only the success of *P. elegans* can be thought of as a woodland development. Despite the length of time between Lateglacial and Holocene deposits, there has been virtually no taxonomic enrichment other than this species which seems to have begun to disperse during the Preboreal (Magnin, in prep.). It is surprising that species that are common in woodlands and potentially available here from the LGI have not benefited from woodland recovery (*A. secale*, *P. pygmaeum*, *C. rugosa* and *C. nemoralis*).

Middle Holocene. – At La Thomassine, the assemblages of zone THOM II, dated to *c.* 8000 cal. a BP, characterize an open woodland, a deciduous oak forest as indicated by charcoal analysis. Compared with the Early Holocene assemblages (MIR-5 II), they include, alongside a very abundant population of *P. elegans*, more strictly woodland species: *A. aculeata*, *M. obscura*, *C. nemoralis*, *O. clarus* and *C. tridentatum*. In the Mirail valley, the presence of these species can be observed in zone MIR-5 III, which could be synchronous with zone THOM II, but their presence is almost anecdotal in assemblages for they

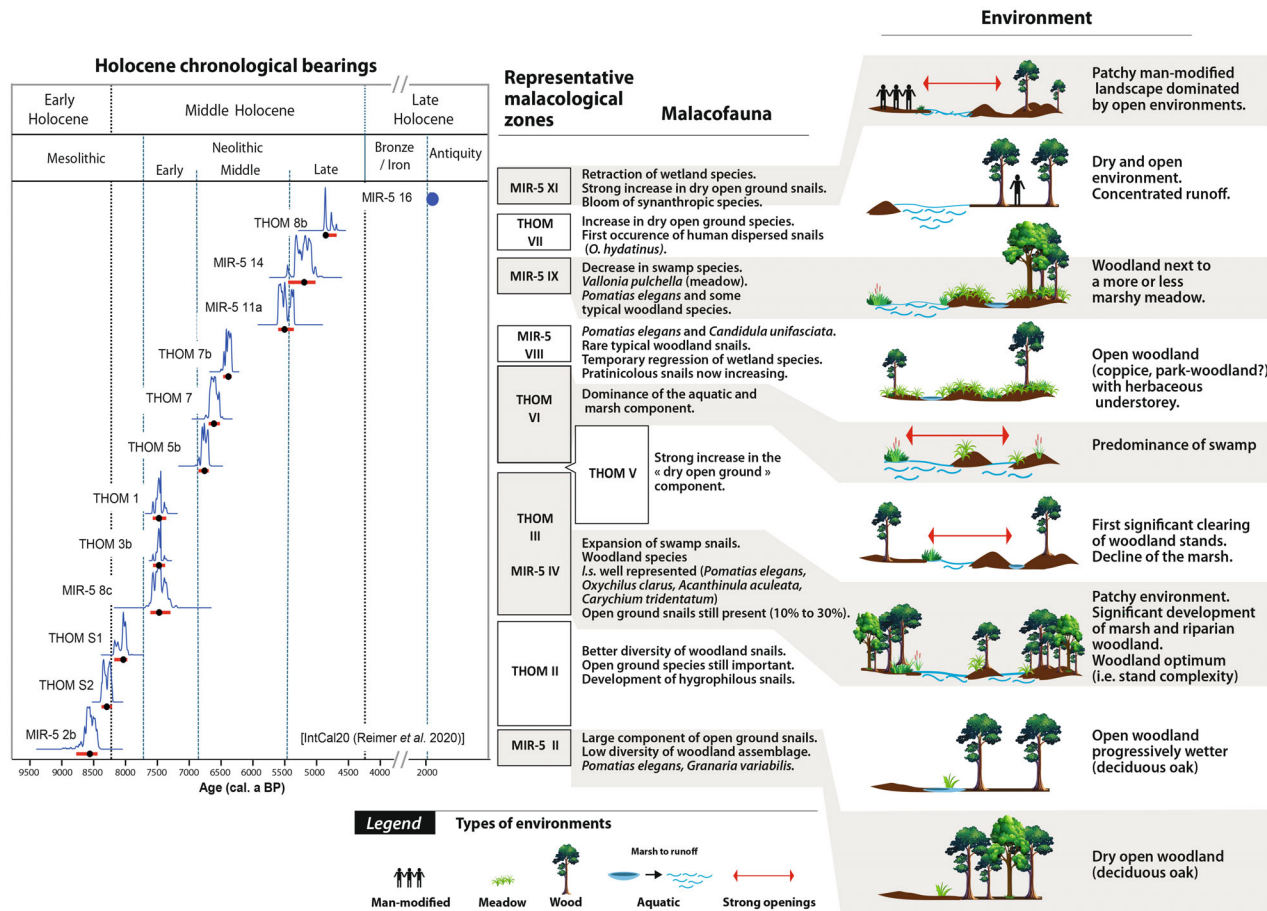


Fig. 10. Summary of the Holocene molluscan succession on the southern slope of the Luberon mountain range.

are suddenly and durably overshadowed by wetland molluscs. A new and final enrichment in woodland species occurred at La Thomassine between *c.* 7500 and *c.* 6600 cal. a BP, first at the very beginning of zone THOM III (*P. pygmaeum*, Vitrinidae sp. indet. (*Phenacolimna major?*) and *M. cantiana*) and then at the beginning of zone THOM IV (*V. pusilla*, *V. luberonensis*, *V. contracta* and *Euomphalia strigella*). In the Mirail succession, it is only at *c.* 5500 cal. a BP, i.e. at the end of the Atlantic, that *O. clarus* and *M. cantiana* appear, and finally we can observe during Late Antiquity the arrival of new, hygrophilic woodland-dwelling species (*M. plicatula* and *H. obvoluta*) within an assemblage from open environment whose heterogeneous constitution is the result of a new, complex landscape structure. The two successions of La Thomassine and Le Mirail (MIR-5) thus show phase shifts in the postglacial recolonization by woodland taxa. For the most part, the assembly of woodland snail communities on the southern slope of the Luberon take place during the Atlantic period, between *c.* 8000 and *c.* 6600 cal. a BP at La Thomassine, but up to *c.* 5500 cal. a BP at Le Mirail. This interval does not exclude later adjustments at Le Mirail, but also and

especially on the Ubac site (northern slope of the Petit Luberon), where the most completed woodland assemblages date from the Early Bronze Age, *c.* 4000 cal. a BP (Martin & Magnin 2002; Martin 2004; Bizot & Sauzade 2015).

Boycott (1934) remarked that woods as such have no characteristic fauna. From an autoecological point of view, woodland species are a heterogeneous assortment, few of which are restricted to woodland (Cameron & Redfern 1972; Evans 1972; Cameron 1978). Our present analysis is based on a broad definition that includes both stenotopic woodland species and those that, living in varied habitats, are nowadays commonly found in woodlands in Mediterranean France. In total, in the two Holocene successions MIR-5 and La Thomassine, there would be at best a dozen stenotopic woodland species, most of them being rather rare. This usual poverty of woodland snail assemblages, which seem immature in view of the classic belief of a primeval high forest during the Mesolithic and part of the Neolithic (Battentier 2022), has already been described in the Aix-en-Provence basin (Magnin *et al.* 2022). This contrasts with diversity hotspots nowadays detected here and

there, but likewise in the Holocene, when they also are observed patchily during unexpected, sometimes late time periods (Renault *et al.* 1996; Berger *et al.* 2000; Martin 2004; Bizot & Sauzade 2015). The pattern is thus: large, low-diversity areas vs. local, high-diversity hot-spots. In general, woodland malacofaunas vary greatly among themselves, even in the same area, with a nestedness of species distribution at different scales (Cameron & Pokryszko 2004; Hylander *et al.* 2005; Horsák *et al.* 2014; Cameron 2016). Most often, the underlined factors relate to the quality of the habitat or the poor dispersal ability of certain species. To this must be added the fragmentation of the species distributions produced by the LGM, then the impact of human activities. This later factor may have slowed down the colonization by forest species from the Neolithic onwards in central Europe (Horsák *et al.* 2019). It must have been all the more effective in the Mediterranean region where it was early added to other constraints such as summer drought.

At site level, the reassembly of postglacial woodland communities in the Luberon does not follow a linear way. Furthermore, it does not completely coincide with the higher proportion of woodland snail shells in the assemblages, nor with the regional woodland cover optimum as recorded by palaeobotanical surveys. It is likely that the dispersal ability of woodland snails, usually low (Baur & Baur 1988; Pfenninger 2002; Hylander 2011; Cameron 2016; Barbato *et al.* 2020a, b), is responsible for the complexity of the observed patterns. In our diachronic approach, it is probable that we observe situations of non-equilibrium as a consequence of more or less random dispersal in a changing environment.

The postglacial colonization by woodland snails in the Mediterranean region: a parallel history to temperate Europe?

Part of the modern malacofauna of temperate Europe would be influenced by its postglacial spread from traditional southern glacial refugia (Limondin-Lozouet & Preece 2014; Juříčková *et al.* 2014). So far, a comparison between southern and temperate Europe has been complicated owing to very uneven data sets and a sparse knowledge of mollusc successions of southern Europe (Juříčková *et al.* 2014). Although southern Europe is characterized by an extraordinary physical and biological diversity, our results concerning the French Mediterranean area can allow to assess the contribution of putative southern macrorefugia to the Holocene dynamics of forest snails in temperate Europe.

The first postglacial appearance of woodland snails is informative. It is most often delayed in the French Mediterranean area. *Pomatias elegans* plays a key role in this region as a pioneer woodland species, either

in Holocene successions or along recent secondary successions (Magnin & Taton 1995; Magnin *et al.* 2022). It is a cold-sensitive snail with a Mediterranean and western European distribution. Its extremely discreet presence in the Lateglacial deposits, *c.* 13 000 cal. a BP, remains to be verified. More certainly its spread started *c.* 10 000 cal. a BP (Magnin, in prep.), first in a steppe landscape, with populations still reduced *c.* 9000 cal. a BP (Magnin *et al.* 2022), then reaching an overwhelming place in open-woodland assemblages from the end of the Boreal period (*c.* 8550 cal. a BP). Absent in central Europe (Juříčková *et al.* 2014), *P. elegans* appears in Holocene successions in Luxembourg *c.* 9200 cal. a BP (Granai *et al.* 2020), in Normandy between *c.* 10 200 and *c.* 9500 cal. a BP (Limondin-Lozouet & Preece 2004; Limondin-Lozouet *et al.* 2005) and in Britain *c.* 8450 cal. a BP (Preece & Bridgland 1998). These dates attest to quasi-simultaneous colonizations between the south and the north. Yet above all, *P. elegans* was not a pioneer species in temperate Europe, which experienced an earlier colonization by more strictly forest taxa. A first colonization wave happened in these regions *c.* 11 300 cal. a BP near the Western Carpathian refugium (Juříčková *et al.* 2018; Frodlová & Horsák 2021) and 1000 years later westwards (Horsák *et al.* 2020). In all these successions, a sharp increase in the colonizing species occurred at the transition from Preboreal to Boreal periods, i.e. while the malacofauna of the Mediterranean region was still largely steppe-like. At least 70% of all forest species appeared before 8200 cal. a BP in temperate Europe (Horsák *et al.* 2020) while the forest malacofauna of SE France generally remained poorly diversified at that time. Among the species that contributed to the development of the forest malacofauna during the Early Holocene in the continental and Atlantic regions of temperate Europe (Limondin-Lozouet & Preece 2004; Limondin-Lozouet *et al.* 2005; Juříčková *et al.* 2014; Horsák *et al.* 2019, 2020; Granai *et al.* 2020), there is a pool of species in common with the malacofauna of Mediterranean France. In this last region, however, such species generally appeared at least 1000 years later (*M. obscura*) or have remained confined, sometimes until the present day, in sites with propitious conditions (e.g. *Discus rotundatus*, *Aegopinella pura*, *Sphyradium dolium*). The case of *Discus rotundatus* is revealing. The appearance of this species at the beginning of the Holocene, in the successions of temperate Europe, corresponds to the development of the forest component in the malacological assemblages, between *c.* 10 200 and *c.* 9500 cal. a BP (Preece 1997; Meyrick 2001; Limondin-Lozouet & Preece 2004; Limondin-Lozouet *et al.* 2005; Granai *et al.* 2020). This common European species, which lives in moist litter under deciduous forests, is absent from the Holocene successions of the Luberon (this paper) and those of Aix-en-Provence (Magnin 1991; Magnin *et al.* 2022). In the Mediterranean

region, its populations are generally localized, nowadays and throughout the Holocene. This patchy distribution testifies to a difficult colonization or recolonization. This is due to the combination of factors already mentioned: severity of a cold and dry LGM, low dispersal ability, aridity of the Mediterranean bioclimate, age and intensity of anthropization. The case of *D. rotundatus* applies to the majority of strictly forest species in Provence, excepting the more widespread *M. obscura* and *A. aculeata*.

All these observations further weaken the hypothesis of a Holocene colonization of temperate Europe by cold-sensitive forest snails from southern – or at least Mediterranean – macrorefugia via the Rhodanian corridor, contrary to the pattern described for other interglacials (Rousseau 1989, 1992; Limondin-Lozouet *et al.* 2020). They add to the increasing collection of evidence which demonstrates the importance of northern refugia for forest snails (Juříčková *et al.* 2014, 2014; Horsák *et al.* 2019, 2020). Furthermore, the Mediterranean region itself has not benefited from the macrorefugia that it would have sheltered or with which it would have been close. As in the case of temperate Europe, local, scattered microrefugia probably largely contributed to its recolonization by forest species. The survival without expansion of *Retinella olivetorum* in the vicinity of Aix-en-Provence, since the last interglacial (Magnin *et al.* 2012), is direct evidence of such microrefugia.

Evaluating the structure of Holocene woodlands

Evaluating the structure of Holocene woodlands is a critical issue given the difference in perception that may exist between pollen analysis and some other proxies when it comes to reconstructing the structure of Holocene woodlands (Mitchell 2005), particularly in Mediterranean Europe (Grove & Rackham 2001). Fortunately, habitat structure is a key factor to explain land snail distribution and abundance (Magnin 1991; Magnin & Tatonni 1995; Labaune & Magnin 2001; Menez 2007), including that of woodland (Barbato *et al.* 2020a, b; Gheoca *et al.* 2023). Assemblages of terrestrial molluscs therefore have a valuable potential to reconstruct the structure of Holocene local stands (Preece *et al.* 1986; Mitchell 2005), in addition to palaeobotanical data which provide information on vegetation composition (Battentier 2022), often at a larger scale.

At the end of the Boreal (MIR-5 II), the malacofauna indicates an open woodland in a dry context (Fig. 10). Charcoal analysis shows this is a deciduous oak stand (Beauvais & Cazorla *in* Martin 2004). The woodland interpretation of snail assemblages is mainly deduced from the abundance of *P. elegans*. It is difficult to determine whether the absence of stenotopic woodland species is due to the open structure of the vegetation or to the delayed assembly of the woodland snail communities

on site. It is therefore, above all, the importance of open ground snails – potentially the anti-woodland species of Boycott (1934) – that may indicate the degree of openness. However, it would be necessary to determine to what extent the species assigned to the open ground category are really anti-woodland species. This category is dominated by *G. variabilis*, a species common in the loess of Provence and abundant in the Lateglacial deposits of Le Mirail. It is clearly a saxicolous and xerophilous snail, not sun-sensitive (Germain 1930; Welter-Schultes 2012). Nevertheless, as already noted, it sometimes tolerates a significant tree cover (i.e. woody plants >2 m), up to 30 or 40% (Magnin 1991). In this zone MIR-5 II, the peak of abundance of *V. costata*, another recognized open ground snail, which occasionally lives in woodland (Evans 1972), coincides with that of *P. elegans* and therefore is probably linked to the presence of a woodland. In addition, there does not appear to be a significant herbaceous cover, otherwise species such as *C. unifasciata* or *X. cespitum* (and even *X. geyeri*) would be better represented.

At the beginning of the Atlantic (*c.* 8000 cal. a BP), the woodland at La Thomassine – always a deciduous oak woodland – appears progressively more closed and moister. *Granaria variabilis* still dominates the open ground component, but the diversity of woodland species is greater. This reflects a more advanced recolonization but also, most likely, a complex habitat structure. This development is still increasing in zone THOM III corresponding to the Early Neolithic. Holocene assemblages are then comparable with those that can be observed nowadays, downstream from the site, in the thalweg occupied by a mosaic of complex woody stands (i.e. 30–40% high woody plants; 15–20% low woody plants) and narrow *Phragmites* meadows (Magnin, unpublished data). It is during this period, *c.* 7500 to 7400 cal. a BP, that the woodland cover appears to reach its greatest complexity, even if the canopy does not seem to be very closed. On the northern slope of the Petit Luberon, the optimum was reached *c.* 7880 cal. a BP with an open woodland, which became even more open and drier from *c.* 7570 cal. a BP (Martin & Magnin 2002; Martin 2004). This same woodland optimum is found further south, in Aix-en-Provence, between *c.* 8000 and *c.* 6700 cal. a BP (Magnin *et al.* 2022). In these sites, the successions are comparable with those of the Luberon, but the assemblages included, as early as 7000 cal. a BP, rare shells of xero-thermophilic and synanthropic Mediterranean snails (e.g. *Cermea virgata*). After this optimum, at La Thomassine, despite the growth of the swamp, we can observe a decrease in woodland cover which proceeds in fits and starts. In the Mirail tufa (MIR-5), on the other hand, it is impossible to describe the structure of the woodland during the maximum development of the swamp. It is only from zone MIR-5 V, at the end of the Atlantic period, that we can attempt to glimpse it. Malacological assemblage 11b

(c. 5470 cal. a BP) dominated by *P. elegans*, *C. unifasciata* and *V. costata* evokes an immature woodland, of the park-woodland type, sufficiently open to promote a good cover of herbaceous vegetation. This depleted assemblage has similarities to those of the Late Boreal, but the praticalous *C. unifasciata* here replaces the saxicolous *G. variabilis*. After this stage, snail assemblages first show the return of a riparian woodland, i.e. a wetter habitat with a more complex structure. It is then substituted by a drier and more open park-woodland vegetation, with a dominant herbaceous layer (base of zone MIR-5 X). To some extent, it is a reproduction of zone MIR-5 VIII, but with a more open horizontal structure. The discrete reappearance of a riparian woodland then constitutes, c. 5000 cal. a BP, the last woodland occurrence in the MIR-5 succession.

Our results correlate well overall with those accumulated over decades by palaeobotanists (Battentier 2022). In terms of structure of the woodlands at their optimum, they provide some clarifications and things to consider. If the beginning of the Early Holocene, before 8500 cal. a BP, is represented in the successions here studied, it can only be at the base of La Thomassine section (THOM I) whose assemblage indicates a more or less wooded steppe vegetation consistent with the anthracozone 1b of Heinz and Thiébault (1998). This period, characterized by a sandy-silty sedimentation, is better represented elsewhere in Basse-Provence where it predates pre-forest stages (Magnin *et al.* 2022). The Late Boreal oak woodland (MIR-5 II) stays open and immature. To qualify it, open woodland seems more appropriate than forest, which some authors use in the sense of primeval forest, i.e. mature forest (Battentier 2022). Later, between c. 8000 and c. 7400 cal. a BP, woodlands reached their optimum at the end of a succession promoted by a more humid environment. This result confirms the evolution described in the Aix-en-Provence area (Magnin *et al.* 2022). It is consistent with regional palaeobotanical data (Triat-Laval 1978; Thiébault 1997; Delhon 2005; Delhon *et al.* 2010; Battentier *et al.* 2018; Battentier 2022). Surprisingly, however, even during this optimum, the canopy is quite open, with probably less than 50% cover.

Identifying imprints of human activities on snail communities and habitats

Land snails are sensitive to changes induced by human activities. They are first indirectly affected by the modification of their habitats at the station scale (Evans 1972; Magnin & Taton 1995; Labaune & Magnin 2002; Hylander 2011; Douglas *et al.* 2013) but also by changes at the landscape level (Magnin *et al.* 1995; Aubry & Magnin 2005). Furthermore, community composition can be directly modified by the development of synanthropic species whose passive dispersal is facilitated, and which are often introduced either

intentionally or accidentally (Magnin & Martin 2012; Nurinisyah *et al.* 2016). In Holocene successions, the causal relationship between environmental change and anthropogenic disturbance may be difficult to establish (Preece *et al.* 1986). This can be considered in two ways: (i) when malacological assemblages indicate changes in the structure of plant formations that cannot be explained by the known amplitude of climatic variations (Magnin & Martin 2008); and (ii) when introduced or clearly synanthropic species develop. In both cases, the presence of archaeological data or other evidence of human activities is a corroborating argument.

In the Mirail (MIR-5) and La Thomassine successions, snail communities and their habitats seem to be impacted by human activities on several occasions (Fig. 10). The open and immature features of woodlands during the Late Boreal and Early Atlantic raise questions. On the one hand, the malacological assemblages could express the logical proceedings of a succession influenced by a climatic trend from dry to wetter conditions between c. 8550 and 8000 cal. a BP. The woodlands of zone MIR-5 II, particularly open and dry, seem to be the succession stage following the steppe landscape that persisted in Basse-Provence until c. 9000 cal. a BP (Magnin *et al.* 2022). As for zone THOM II of La Thomassine, it would represent the woodland optimum we have described. However, the related sediments are rich in charcoal (deciduous *Quercus* dominant) and contain heated pebbles and reddened soil aggregates that evoke fires or the emptying of hearths. The possibility of a local human impact must be considered. Even if the impact of Mesolithic hunter-gatherers on the landscape has long been controversial (Roberts *et al.* 2018) and is generally considered to be minimal, this hypothesis should not be completely rejected. It could partly explain the relatively open structure forest stands at their optimum. Elsewhere in Provence, at Tourves, a human impact has been detected by pollen analysis at 7880 cal. a BP, while beetle assemblages do not record it (Nicol-Pichard 1987; Andrieu-Ponel & Ponel 1999). Several studies have revived the debate in continental Europe and Great Britain (Innes & Blackford 2003; Bishop *et al.* 2015; Dietze *et al.* 2018; Heidgen *et al.* 2022). On SE Iberian Peninsula, Sánchez-García *et al.* (2024) suggest, from the coincidence of the highest charcoal accumulation rates with Late Mesolithic activity, even during periods of predominance of oak forest, that hunter-gatherer communities transformed the landscape by burning woodlands. Further investigations are needed to assess this hypothesis in Provence.

At La Thomassine, the first signs of woodland opening attributable to anthropization appear at the end of zone THOM III (during the Early Neolithic, c. 7450 cal. a BP). They continue in zone THOM IV. The impact of human activities becomes conspicuous in zone THOM V during which a clear decline in woodland coincides with a

detrital accumulation containing uncountable charcoal fragments, together with some artefacts and other evidence of human activities. This episode is attributable to the Early-Middle Neolithic, 6834 to 6671 cal. a BP. Open woodland vegetation then quickly regenerates (level 6). In the Mirail valley (MIR-5), it is only from the Late Neolithic, c. 5470 cal. a BP, that the malacological signal of anthropization becomes clear, but it is also at the moment when the reduction of the swamp area begins, allowing the observation of a wider environment. Earlier assemblages already included a few snails indicating the existence of open, dry habitats at the edge of the swamp. This presence of a xerophilous malacofauna in the Atlantic may be an indication of anthropization. Although discontinuous, the progress of *C. unifasciata* from zone MIR-5 VIII to the end of the succession is a much more significant element, this species being nowadays dominant in the dry grasslands of the Grand Luberon below 900–1000 m a.s.l. (Labaune & Magnin 2002). The development of *C. unifasciata* occurs in three increasingly pronounced pulses. Initially (zone MIR-5 VIII), we probably are in the presence of a park-woodland with an abundant herbaceous layer. This episode shortly preceded the appearance of the first shards of Neolithic pottery. During the next pulse (zone MIR-5 X), anthropization interrupts the return of the riparian woodland for a while. Anthropization is even clearer after a Late Neolithic settlement dated at c. 5160 cal. a BP. In the same way, the Late Neolithic period at La Thomassine is characterized, c. 4800 cal. a BP, by a progression of species from dry open environments, including *O. hydatinus*, a species introduced to Provence during this period. Finally, in the Late Antiquity assemblages of the Mirail section, open ground snails account for more than 75%. With this last stage (zone MIR-5 XI) a threshold is crossed. The artificialization of the landscape and its heterogeneity are suggested by the miscellaneous nature of the malacofauna, which includes synanthropic species (*O. draparnaudi*), human-dispersed mesophilic species (*T. hispidus*), open ground species (introduced *O. hydatinus*), and even some stenotopic woodland snails. This pattern has already been described in the Aix-en-Provence region (Bonnet *et al.* 2020; Magnin *et al.* 2022).

In the two successions studied here, anthropization stages highlighted by the malacofauna are in line with the regional evolution described by palaeobotany (Battentier *et al.* 2018; Battentier 2022). Anthropization remained discrete and difficult to characterize during the Early Neolithic. In the Middle Neolithic, a major erosive event associated with a significant opening of woodland is highlighted at La Thomassine. From the Late Neolithic period, in the two sites, human impact is evident. It coincides with changes in the composition of snail communities. In the Tourves wetland, 50 km SE of the Luberon, it was also during the Late Neolithic that human impact led to a drastic environmental change

recorded by beetle assemblages (Andrieu-Ponel & Ponel 1999). However, there are substantial differences, regarding the malacofauna, between the sites in Haute-Provence and those of Basse-Provence, only 40 km further south. Around Aix-en-Provence, malacofauna reveals a more marked anthropization of the landscape from 7000 or 6500 cal. a BP (Magnin *et al.* 2022). In addition, most of the synanthropic species so characteristic of anthropization and landscape opening in Basse-Provence and Languedoc (Martin 2004; Martin *et al.* 2005; Magnin & Martin 2012; Magnin *et al.* 2022), are absent from the Luberon successions. This is the case of *C. virgata*, an emblematic synanthropic species that has been present near the coast (Châteauneuf-les-Martigues) since the Early Neolithic (7227 to 7165 cal. a BP), and which appears at Aix-en-Provence at the same time (7336 to 7247 cal. a BP). These regional differences may be explained by a lower intensity of human impact in the Luberon during the Neolithic. They are also due to a less Mediterranean character, the regional malacofauna being affected by a strong biogeographical gradient towards the SW (Magnin & Taton 1995; Kiss *et al.* 2004). The singular palaeoenvironmental dynamics reported at Martigues from the Early Neolithic onwards thus represent an extreme situation in which the climatic and edaphic conditions near the coast of western Provence would not have allowed the deciduous oak forest to become dominant (Battentier *et al.* 2020; Battentier 2022).

Conclusions

Study of these three mollusc successions, on the edge of the southern Alps, fills a gap in our knowledge of the Quaternary malacofauna of the French Mediterranean region. The Lateglacial malacofauna is described for the first time. Its most prominent feature, compared with Pleniglacial, is the important development of hygrophilic communities. Despite an increasing species richness and some signs of warming and increasing humidity, interpreting climate variations from the malacofauna is challenging. The same applies to the evolution of vegetation cover. Changes are not contrasting and the impoverished communities, mainly inherited from the LGM, may be transient and unadjusted. Nevertheless, even in the hypothesis of nonequilibrium communities, it is not conceivable to interpret LGI assemblages as compatible with the deciduous oak woodland mentioned by some authors. They are, however, compatible with a patchy steppe landscape with some restricted wetlands. Younger Dryas would reflect a severe aridification without cooling.

The reassembly of forest snail communities has been laborious throughout the postglacial. It did not take advantage of the glacial refugia that the Mediterranean region sheltered. Compared with northern Europe, the first strictly forest species appeared 1000 years later.

Their number first increased *c.* 8000 cal. a BP, then several times until the beginning of the historical period. This recolonization was affected by temporal shifts between sites and a great spatial heterogeneity. This resulted in a pattern of large, low-diversity areas vs. local, high-diversity hotspots still observed today. Early anthropization and Mediterranean aridity have been added here to other constraints already recognized in temperate Europe, e.g. impoverishment and fragmentation of communities owing to the LGM, distance to refugia, low dispersal ability and variations in habitat quality.

Regarding woodland cover during the Holocene, our results correlate well overall with the timing obtained by palaeobotanists. However, the structure of these woodlands seems to have remained quite open, even at their optimum *c.* 7500 to 7400 cal. a BP.

Likewise, anthropization stages pointed out by the malacofauna are in line with the regional evolution described by other proxies. A local impact of Mesolithic hunter–gatherers should not be rejected pending further evidence. Anthropization was low in the Early Neolithic but became more evident during the Early-Middle Neolithic, and more extensive from the Late Neolithic. The consequences of human activities on snail communities and vegetation are less pronounced in the Luberon than in Basse-Provence (Magnin *et al.* 2022), possibly owing to a reduction in aridity. The high variability of the Mediterranean region makes further studies on the Alpine and eastern borders of the French Mediterranean region essential.

Acknowledgements. – We are grateful to the staff of the Parc Naturel Régional du Luberon (PNRL) and Domaine de la Thomassine (Maison de la Biodiversité) for their warm welcome and their invaluable help during fieldwork. Several radiocarbon measurements have been financed by the PNRL. Others were supported from the personal funds of the first author. We are grateful to the two reviewers, including Lucie Juričková, for their useful suggestions or comments, and to Professor Jan A. Piotrowski for editing this paper.

Author contributions. – The project was designed by FM, SM, VO and NS. Field work was done by FM, SM, VO and NS. Geomorphological and sedimentological observations were made by VO and NS. FM and SM conducted the molluscan and data analyses. FM wrote the draft of the manuscript. NS and FM produced the figures SM, VO, NS and FM reviewed and edited the manuscript.

Data availability statement. – Data sharing is not applicable to this article as no new data were created or analyzed in this study.

References

- Alexandrowicz, W. P. 2004: Molluscan assemblages of Late Glacial and Holocene calcareous tufas in Southern Poland. *Folia Quaternaria* 75, 3–309.
- Andrieu-Ponel, V. & Ponel, P. 1999: Human impact on Mediterranean wetland Coleoptera: an historical perspective at Tourves (Var, France). *Biodiversity and Conservation* 8, 391–406.
- Ant, H. 1966: Die Bedeutung der Eiszeiten für die rezente Verbreitung der europäischen Landgastropoden. *Malacologia* 5, 61–62.
- Aubry, S. 2003: *Factors controlling the structure of land snail communities on limestone mountains in South-Eastern France*. Ph.D. thesis, University of Cambridge, 264 pp.
- Aubry, S. & Magnin, F. 2005: Factors structuring land snail communities in south-eastern France: a comparison of two estimation methods. *Ecologia Mediterranea* 31, 65–74.
- Aubry, S., Magnin, F., Bonnet, V. & Preece, R. C. 2005: Multi-scale altitudinal patterns in species richness of land snail communities in South-Eastern France. *Journal of Biogeography* 32, 985–998.
- Barbato, D., Benocci, A. & Manganelli, G. 2020a: Does forest age affect soil biodiversity? Case study of land snails in Mediterranean secondary forests. *Forest Ecology and Management* 455, 117693, <https://doi.org/10.1016/j.foreco.2019.117693>.
- Barbato, D., Benocci, A. & Manganelli, G. 2020b: Corrigendum to “does forest age affect soil biodiversity? Case study of land snails in Mediterranean secondary forests” [For. Ecol. Manage. 455 (2020) 117693]. *Forest Ecology and Management* 461, 117852, <https://doi.org/10.1016/j.foreco.2019.117852>.
- Battentier, J. 2022: *De la mer à la montagne: premiers systèmes d'élevage et paysage végétal de part et d'autre des Alpes méridionales à la fin de la Préhistoire (6500–2000 av. n. è.) – approche anthracologique*. 143 pp. Société préhistorique française, Paris.
- Battentier, J., Binder, D., Guillon, S., Maggi, R., Negrino, F., Sénépart, I., Tozzi, C., Théry-Parisot, I. & Delhon, C. 2018: The environment of the last hunters-gatherers and first agro-pastoralists in the Western Mediterranean region, between the Rhone and the Northern Apennines (7th–6th millennium cal. BCE): attractiveness of the landscape units and settlement patterns. *Quaternary Science Reviews* 184, 167–182.
- Battentier, J., Thiébault, S., Binder, D., Courtin, J., Sénépart, I., Bouby, L., Théry-Parisot, I. & Delhon, C. 2020: L'évolution du couvert forestier et son exploitation mésolithique et néolithique à la Font-aux-Pigeons (Châteauneuf-les-Martigues, Bouches-du-Rhône): apports de l'anthracologie. *Quaternaire* 31, 263–280.
- Baur, A. & Baur, B. 1988: Individual movement patterns of the minute land snail *Punctum pygmaeum* (Draparnaud). *Veliger* 3, 372–376.
- Beaulieu, J.-L., Miras, Y., Andrieu-Ponel, V. & Guiter, F. 2005: Vegetation dynamics in North-Western Mediterranean regions: instability of the Mediterranean bioclimate. *Plant Biosystems* 139, 114–126.
- Berger, J.-F., Magnin, F., Thiébault, S. & Vital, J. 2000: Emprise et déprise culturelle à l'Age du Bronze: l'exemple du Bassin Valdainais (Drôme) et de la moyenne vallée du Rhône. *Bulletin de la Société préhistorique française* 97, 95–119.
- Bilton, D. T., Mirol, P. M., Mascheretti, S., Fredga, K., Zima, J. & Searle, J. B. 1998: Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265, 1219–1226.
- Binder, D., Lanos, P., Angeli, L., Gomart, L., Guilaine, J., Manen, C., Maggi, R., Muntoni, I., Panelli, C. & Radi, G. 2017: Modelling the earliest north-western dispersal of Mediterranean Impressed Wares: new dates and Bayesian chronological model. *Documenta Praehistorica* 44, 54–77.
- Bishop, R. R., Church, M. J. & Rowley-Conwy, P. A. 2015: Firewood, food and human niche construction: the potential role of Mesolithic hunter–gatherers in actively structuring Scotland's woodlands. *Quaternary Science Reviews* 108, 51–75.
- Bizot, B. & Sauzade, G. (eds.) 2015: *Le dolmen de l'Ubac à Goult (Vaucluse): archéologie, environnement et évolution des gestes funéraires dans un contexte stratifié*. 248 pp. Société préhistorique française, Paris.
- Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G. & Fontaine, C. 2010: *The Mediterranean Region: Biological Diversity in Space and Time*. 376 pp. OUP, Oxford.
- Bonifay, E. 1962: *Recherches sur les terrains quaternaires dans le Sud-Est de la France*. 194 pp. Delmas, Bordeaux.
- Bonnet, S., Magnin, F. & Aujaleu, A. 2020: Évolution des paysages et réflexion sur les modalités d'exploitation des sols. *Revue archéologique de Narbonnaise* 53, 13–29.

- Boschi, C. 2011: *Die Schneckenfauna der Schweiz. Ein umfassendes Bild- und Bestimmungsbuch*. 624 pp. Haupt Verlag, Bern, Stuttgart & Wien.
- Bourdier, F. 1961: *Le bassin du Rhône au Quaternaire: géologie et préhistoire*. 364 & 294 pp. CNRS, Paris.
- Boycott, A. E. 1934: The habitats of land Mollusca in Britain. *The Journal of Ecology* 22, 1–38.
- Brennan, R. & Quade, J. 1997: Reliable Late-Pleistocene stratigraphic ages and shorter groundwater travel times from ^{14}C in fossil snails from the southern great basin. *Quaternary Research* 47, 329–336.
- CNRS, ER. 30 1975: *Marseille. Carte climatique détaillée de la France*. 6 pp. Ophrys, Gap & Paris.
- Cameron, R. A. D. 1978: Interpreting buried land-snail assemblages from archaeological sites – problems and progress. In Brothwell, D. R., Thomas, K. D. & Clutton-Brock, J. (eds.): *Research Problems in Zooarchaeology*, 19–23. Institute of Archaeology, London.
- Cameron, R. A. D. 2016: *Slugs and Snails*. 508 pp. William Collins, London.
- Cameron, R. A. D. & Pokryszko, B. M. 2004: Land mollusc faunas of Białowieża Forest (Poland), and the character and survival of forest faunas in the North European Plain. *Journal of Molluscan Studies* 70, 149–164.
- Cameron, R. & Redfern, M. 1972: The terrestrial Mollusca of the Malham area. *Field Studies* 3, 589–602.
- Carter, S. P. 1990: The stratification and taphonomy of shells in calcareous soils: implications for land snail analysis in archaeology. *Journal of Archaeological Science* 17, 495–507.
- Cambourieu-Nebout, N., Peyron, O., Dormoy, I., Desprat, S., Beaudouin, C., Kotthoff, U. & Marret, F. 2009: Rapid climatic variability in the west Mediterranean during the last 25 000 years from high resolution pollen data. *Climate of the Past* 5, 503–521.
- Davies, P. 2008: *Snails: Archaeology and Landscape Change*. 199 pp. Oxbow Books, Oxford.
- Davies, P. & Griffiths, H. I. 2005: Molluscan and ostracod biostratigraphy of Holocene tufa in the Test valley at Bossington, Hampshire, UK. *The Holocene* 15, 97–110.
- Delhon, C. 2005: *Anthropisation et paléoclimats du Tardiglaciaire à l'Holocène en moyenne vallée du Rhône : études pluridisciplinaires des spectres phytolithiques et pédo-anthracologiques de séquences naturelles et de sites archéologiques*. Ph.D. thesis, Université Paris 1, 778 pp.
- Delhon, C., Thiébaud, S., Brochier, J.-L. & Berger, J.-F. 2010: Dynamiques de végétation au Tardiglaciaire et à l'Holocène ancien en moyenne vallée du Rhône d'après les données anthracologiques. *Quaternaire* 21, 281–293.
- Dietze, E., Theuerkauf, M., Bloom, K., Brauer, A., Dörfler, W., Feeser, I., Feurdean, A., Gedminienė, L., Giesecke, T., Jahns, S., Karpińska-Kolaczek, M., Kolaczek, P., Lamentowicz, M., Latalowa, M., Marcisz, K., Obremska, M., Pędziszewska, A., Poska, A., Rehfeld, K., Stančíkaiūtė, M., Stivrins, N., Święta-Musznicka, J., Szał, M., Vassiljev, J., Veski, S., Wacnik, A., Weisbrodt, D., Wiethold, J., Vannièr, B. & Słowiński, M. 2018: Holocene fire activity during low-natural flammability periods reveals scale-dependent cultural human-fire relationships in Europe. *Quaternary Science Reviews* 201, 44–56.
- Douglas, D. D., Brown, D. R. & Pederson, N. 2013: Land snail diversity can reflect degrees of anthropogenic disturbance. *Ecosphere* 4, art28, <https://doi.org/10.1890/ES12-00361.1>.
- Dubar, M. 1983: *Stratigraphie des dépôts du Néogène supérieur et du Pléistocène du bassin de la moyenne Durance; interprétations géodynamiques et paléogéographiques*. Ph.D. thesis, Université Aix-Marseille I, 428 pp.
- Dumas, M. (ed.) 2013: *Le Luberon, encyclopédie d'une montagne provençale. Tome 1. Milieu naturel, histoire et peuplements*. 342 pp. Les Alpes de Lumière, Forcalquier.
- Ermolli, E. R., Masi, A., Vignola, C., Di Lorenzo, H., Masci, L., Bona, F., Forti, L., Lembo, G., Mazzini, I., Mecozzi, B., Muttillo, B., Pieruccini, P., Sardella, R. & Sadori, L. 2022: The pollen record from Grotta Romanelli (Apulia, Italy): new insight for the Late Pleistocene Mediterranean vegetation and plant use. *Review of Palaeobotany and Palynology* 297, 104577, <https://doi.org/10.1016/j.revpalbo.2021.104577>.
- Evans, J. G. 1972: *Land Snails in Archaeology: With Special Reference to the British Isles*. 436 pp. Seminar Press, London.
- Evans, J. G. 1991: An approach to the interpretation of dry-ground and wet-ground molluscan taxocenes from Central-Southern England. In Harris, D. R. & Thomas, K. D. (eds.): *Modelling Ecological Change*, 75–89. Institute of Archaeology, London.
- Falkner, G., Ripken, T. E. J. & Falkner, M. 2002: *Mollusques continentaux de France: liste de référence annotée et Bibliographie*. 350 pp. Muséum national d'Histoire naturelle, Paris.
- Fiorentino, V., Manganeli, G., Giusti, F. & Ketmaier, V. 2016: Recent expansion and relic survival: Phylogeography of the land snail genus *Helix* (Mollusca, Gastropoda) from South to North Europe. *Molecular Phylogenetics and Evolution* 98, 358–372.
- Frodlová, J. & Horsák, M. 2021: High-resolution mollusc record from the Mituchovci tufa (western Slovakia): a reference for the Holocene succession of Western Carpathian mid-elevation forests. *Boreas* 50, 709–722.
- Gargominy, O., Prie, V., Bichain, J.-M., Cucherat, X. & Fontaine, B. 2011: Liste de référence annotée des mollusques continentaux de France. *MalaCo* 7, 307–382.
- Germain, L. 1930: *Mollusques terrestres et fluviatiles t.1*. 477 pp. Paul Lechevalier, Paris.
- Gheoca, V., Benedek, A. M. & Schneider, E. 2023: Taxonomic and functional diversity of land snails reflects habitat complexity in riparian forests. *Scientific Reports* 13, 9808, <https://doi.org/10.1038/s41598-023-36896-6>.
- Granai, S., Dabkowski, J., Hájková, P., Naton, H.-G. & Brou, L. 2020: Holocene palaeoenvironments from the Diredall tufa (Luxembourg) reconstructed from the molluscan succession and stable isotope records. *The Holocene* 30, 982–995.
- Granier, J. 1976: Les mollusques terrestres du Sud-Est. In de Lumley, H. (ed.): *La Préhistoire Française. Tome I. Les Civilisations Paléolithiques et Mésolithiques de la France*, 447–453. CNRS, Paris.
- Greenacre, M. J. 1984: *Theory and Applications of Correspondence Analysis*. 364 pp. Academic Press, London.
- Grimm, E. C. 2011: Tilia software v. 3.0.1. Available at: <https://www.neotomadb.org/apps/tilia>.
- Grove, A. T. & Rackham, O. 2001: *The Nature of Mediterranean Europe: An Ecological History*. 324 pp. Yale University Press, New Haven, London.
- Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001: PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 1–9.
- Heidgen, S., Marinova, E., Nelle, O., Ebner, M., Rotava, T., Tafelmaier, Y., Krauß, R., Bofinger, J. & Junginger, A. 2022: Palaeoecological signals for Mesolithic land use in a Central European landscape? *Journal of Quaternary Science* 37, 1164–1179.
- Heinz, C. & Thiébaud, S. 1998: Characterization and palaeoecological significance of archaeological charcoal assemblages during Late and Post-Glacial phases in Southern France. *Quaternary Research* 50, 56–68.
- Hewitt, G. 1996: Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58, 247–276.
- Hewitt, G. M. 1999: Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68, 87–112.
- Holyoak, D. 1989: The location of refugia for woodland snails during cold stages of the Quaternary. *Quaternary Newsletter* 57, 12–13.
- Horsák, M., Juříčková, L. & Pícka, J. 2013: *Měkkýši České a Slovenské republiky = Molluscs of the Czech and Slovak Republics*. 264 pp. Nakladatelství Kabourek, Zlín.
- Horsák, M., Limondin-Lozouet, N., Granai, S., Dabkowski, J., Divíšek, J. & Hájková, P. 2020: Colonisation dynamic and diversity patterns of Holocene forest snail fauna across temperate Europe: the imprint of palaeoclimate changes. *Quaternary Science Reviews* 240, 106367, <https://doi.org/10.1016/j.quascirev.2020.106367>.
- Horsák, M., Limondin-Lozouet, N., Juříčková, L., Granai, S., Horácková, J., Legentil, C. & Ložek, V. 2019: Holocene succession patterns of land snails across temperate Europe: east to west variation related to glacial refugia, climate and human impact. *Palaeogeography, Palaeoclimatology, Palaeoecology* 524, 13–24.

- Horsák, M., Zelený, D. & Hájek, M. 2014: Land snail richness and abundance along a sharp ecological gradient at two sampling scales: disentangling relationships. *Journal of Molluscan Studies* 80, 256–264.
- Huntley, B. 1988: Glacial and Holocene vegetation history - 20 ky to present. Europe. In Huntley, B. & Webb, T., III (eds.): *Vegetation History*, 341–383. Kluwer, Dordrecht.
- Hylander, K. 2011: The response of land snail assemblages below aspens to forest fire and clear-cutting in Fennoscandian boreal forests. *Forest Ecology and Management* 261, 1811–1819.
- Hylander, K., Nilsson, C., Gunnar Jonsson, B. & Göthner, T. 2005: Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos* 108, 351–361.
- Innes, J. B. & Blackford, J. J. 2003: The ecology of Late Mesolithic woodland disturbances: model testing with fungal spore assemblage data. *Journal of Archaeological Science* 30, 185–194.
- Jongman, R. H., Braak, C. J. F. T. & Tongeren, O. F. R. v. 1995: *Data Analysis in Community and Landscape Ecology*. 299 pp. Cambridge University Press, Cambridge.
- Juričková, L., Horáčková, J. & Ložek, V. 2014: Direct evidence of central European forest refugia during the last glacial period based on mollusc fossils. *Quaternary Research* 82, 222–228.
- Juričková, L., Horsák, M., Horáčková, J., Abraham, V. & Ložek, V. 2014: Patterns of land-snail succession in Central Europe over the last 15,000 years: main changes along environmental, spatial and temporal gradients. *Quaternary Science Reviews* 93, 155–166.
- Juričková, L., Pokorný, P., Hošek, J., Horáčková, J., Květoň, J., Zahajská, P., Jansová, A. & Ložek, V. 2018: Early postglacial recolonisation, refugial dynamics and the origin of a major biodiversity hotspot. A case study from the Malá Fatra mountains, Western Carpathians, Slovakia. *The Holocene* 28, 583–594.
- Kiss, L., Magnin, F. & Torre, F. 2004: The role of landscape history and persistent biogeographical patterns in shaping the responses of Mediterranean land snail communities to recent fire disturbances: response patterns of land snail communities to fire disturbances. *Journal of Biogeography* 31, 145–157.
- Kühne, G., Kosuch, J., Hochkirch, A. & Schmitt, T. 2017: Extra-Mediterranean glacial refugia in a Mediterranean faunal element: the phylogeography of the chalk-hill blue *Polyommatus coridon* (Lepidoptera, Lycaenidae). *Scientific Reports* 7, 43533, <https://doi.org/10.1038/srep43533>.
- Labaune, C. & Magnin, F. 2001: Land snail communities in Mediterranean upland grasslands: the relative importance of four sets of environmental and spatial variables. *Journal of Molluscan Studies* 67, 463–474.
- Labaune, C. & Magnin, F. 2002: Pastoral management vs. land abandonment in Mediterranean uplands: impact on land snail communities. *Global Ecology and Biogeography* 11, 237–245.
- Legendre, P. & Legendre, L. F. J. 1998: *Numerical Ecology*. 853. Elsevier, Amsterdam.
- Limondin-Lozouet, N. & Antoine, P. 2001: Palaeoenvironmental changes inferred from malacofaunas in the Lateglacial and early Holocene fluvial sequence at Conty, northern France. *Boreas* 30, 148–164.
- Limondin-Lozouet, N. & Preece, R. C. 2004: Molluscan successions from the Holocene tufa of St Germain-le-Vasson, Normandy (France) and their biogeographical significance. *Journal of Quaternary Science* 19, 55–71.
- Limondin-Lozouet, N. & Preece, R. C. 2014: Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe. *Journal of Molluscan Studies* 80, 224–237.
- Limondin-Lozouet, N., Dabkowski, J. & Antoine, P. 2020: 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. *Palaeogeography, Palaeoclimatology, Palaeoecology* 560, 110044, <https://doi.org/10.1016/j.palaeo.2020.110044>.
- Limondin-Lozouet, N., Gauthier, A. & Preece, R. C. 2005: Enregistrement des biocénoses de la première moitié de l'Holocène en contexte tufacé à Saint-Germain-le-Vasson (Calvados). *Quaternaire* 16, 255–271.
- Ložek, V. 1964: *Quartärmollusken der Tschechoslowakei*. 374 pp. Rozprawy ČSAV, Praha.
- Magnin, F. 1989: Les distributions pleistocènes et actuelles de *Trochoidea (XeroCLAUSA) geyeri* (Soós, 1926) (Gastropoda, Helicidae) dans le Sud-Est de la France: un exemple de disjonction d'aire liée au réchauffement post-glaciaire. *Bulletin de la Société Géologique de France* 5, 779–786.
- Magnin, F. 1991: *Mollusques continentaux et histoire quaternaire des milieux méditerranéens: Sud-Est de la France, Catalogne*. Ph.D. thesis, Université Aix-Marseille 2, 340 pp.
- Magnin, F. 1992: Variations de température en Provence pendant le Pléistocène supérieur (stades isotopiques 2 et 3) estimées d'après l'analyse d'associations de gastéropodes terrestres. *Comptes Rendus de l'Académie des Sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre* 315, 231–237.
- Magnin, F. 1993a: Competition between two land gastropods along altitudinal gradients in South-Eastern France: neontological and palaeontological evidence. *Journal of Molluscan Studies* 59, 445–454.
- Magnin, F. 1993b: *Trochoidea geyeri* (Soós, 1926) (Pulmonata, Helicidae) in South-Eastern France: ecology, biogeography and Quaternary history. *Scripta Geologica Special Issue* 2, 291–295.
- Magnin, F. 2014: Middle Pleniglacial to Holocene molluscan assemblages in the Marseille-Aubagne basin (Provence, France). *Quaternaire* 25, 113–125.
- Magnin, F. 2023a: A new *Vitrea* species from the Holocene of south-eastern France (Gastropoda: Eupulmonata: Pristilomatidae). *Archiv für Molluskenkunde* 152, 35–42.
- Magnin, F. 2023b: Erratum to Magnin (2023) “A new *Vitrea* species from the Holocene of south-eastern France (Gastropoda: Eupulmonata: Pristilomatidae).” *Archiv für Molluskenkunde* 152, 343–344.
- Magnin, F. & Martin, S. 2008: Grandeur et misère de l'analyse malacologique, ou comment discriminer les facteurs climatiques et anthropiques de l'évolution des paysages holocènes. *Bulletin Archéologique de Provence Supplément* 5, 61–73.
- Magnin, F. & Martin, S. 2012: Escargots synanthropiques et domestication de la nature. Mécanismes, processus et représentations. *Techniques & Culture* 59, 260–283.
- Magnin, F. & Taton, T. 1995: Secondary successions on abandoned cultivation terraces in calcareous Provence. II – The gastropod communities. *Acta Oecologica* 16, 89–101.
- Magnin, F., Bonnet, S. & Cençon-Salvayre, C. 2022: Land snail fauna and Holocene environmental changes in Mediterranean France: a digest from three representative sedimentary sequences. *Quaternary Science Reviews* 276, 107303, <https://doi.org/10.1016/j.quascirev.2021.107303>.
- Magnin, F., Dubar, M. & Kiss, L. 2012: A relict population of *Retinella olivetorum* in southern France. Biogeographical and historical implications. *Journal of Conchology* 41, 37–48.
- Magnin, F., Taton, T., Roche, P. & Baudry, J. 1995: Gastropod communities, vegetation dynamics and landscape changes along an old-field succession in Provence, France. *Landscape and Urban Planning* 31, 249–257.
- Martin, S. 2004: *Caractérisation de l'anthropisation à l'Holocène en Provence et en Languedoc oriental, par les mollusques terrestres*. Ph.D. thesis, Université Paris 1, 429 pp.
- Martin, S. & Magnin, F. 2002: Caractérisation des perturbations anthropiques dans la séquence holocène de l'Ubac (Goult, Vaucluse), à partir de la malacofaune. In Richard, H. & Vignot, A. (eds.): *Équilibres et ruptures dans les écosystèmes depuis 20 000 ans en Europe de l'Ouest*, 205–212. Les Belles Lettres – Presses Universitaires de France, Paris.
- Martin, S., Magnin, F. & Chevillot, P. 2005: Mise en évidence des discontinuités spatiales et temporelles dans l'anthropisation de la plaine de la Vistrenque à Nîmes (Gard) durant l'Holocène – Apport de l'analyse malacologique. *Quaternaire* 16, 339–352.
- Mazenot, G. 1956: Recherches sur les faunes malacologiques du lœss récent würmien et de divers limons terrestres holocènes dans le Sud-Est de la France. *Publications de la Société Linnéenne de Lyon* 25, 9–24.
- Médail, F. & Diadema, K. 2009: Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* 36, 1333–1345.

- Menez, A. 2007: A new approach to studying and sampling land molluscs: habitat structure and the effects of scale on land molluscs. *Journal of Conchology* 39, 321–327.
- Meyrick, R. A. 2001: The development of terrestrial mollusc faunas in the 'Rheinland region' (western Germany and Luxembourg) during the Lateglacial and Holocene. *Quaternary Science Reviews* 20, 1667–1675.
- Meyrick, R. A. & Karrow, P. F. 2007: Three detailed, radiocarbon-dated, Holocene tufa and alluvial fan mollusc successions from southern Ontario: the first in northeastern North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243, 250–271.
- Michaux, J. R., Magnanou, E., Paradis, E., Nieberding, C. & Libois, R. 2003: Mitochondrial phylogeography of the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Molecular Ecology* 12, 685–697.
- Mitchell, F. J. G. 2005: How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 93, 168–177.
- Moine, O., Antoine, P., Hatté, C., Landais, A., Mathieu, J., Prud'homme, C. & Rousseau, D.-D. 2017: The impact of Last Glacial climate variability in West-European loess revealed by radiocarbon dating of fossil earthworm granules. *Proceedings of the National Academy of Sciences of the United States of America* 114, 6209–6214.
- Nicol-Pichard, S. 1987: Analyse pollinique d'une séquence tardi et postglaciaire à Tourves (Var, France). *Ecologia Mediterranea* 13, 29–42.
- Nurinsyah, A. S., Fauzia, H., Hennig, C. & Hausdorf, B. 2016: Native and introduced land snail species as ecological indicators in different land use types in Java. *Ecological Indicators* 70, 557–565.
- Ollivier, V. 2006: *Continuités, instabilités et ruptures morphogéniques en Provence depuis la dernière glaciation: travertinisation, détritisme et incisions sur le piémont sud du Grand Luberon (Vaucluse, France): relations avec les changements climatiques et l'anthropisation*. Ph.D. thesis, Université Aix-Marseille 1, 357 pp.
- Ollivier, V., Magnin, F., Ali, A., Balme, C. & Frapa, P. 2015: Le tuf calcaire de la Thomassine: paysages et climats du Néolithique ancien dans les collines de Manosque. *Courrier scientifique du Parc naturel régional du Luberon* 13, 44–57.
- Ollivier, V., Magnin, F., Guendon, J.-L. & Miramont, C. 2014: Regards sur les dynamiques paysagères du Pléistocène supérieur du Luberon et de Basse Provence (SIM 3 et SIM 2, France). *Quaternaire* 25, 91–111.
- Pfenninger, M. 2002: Relationship between microspatial population genetic structure and habitat heterogeneity in *Pomatias elegans* (O.F. Müller 1774) (Caenogastropoda, Pomatiasidae). *Biological Journal of the Linnean Society* 76, 565–575.
- Pfenninger, M., Posada, D. & Magnin, F. 2003: Evidence for survival of Pleistocene climatic changes in Northern refugia by the land snail *Trochoidea geyeri* (Soós 1926) (Helicellinae, Stylommatophora). *BMC Evolutionary Biology* 3, 8, <https://doi.org/10.1186/1471-2148-3-8>.
- Pigati, J. S., McGeehin, J. P., Muhs, D. R. & Bettis, E. A. 2013: Radiocarbon dating late Quaternary loess deposits using small terrestrial gastropod shells. *Quaternary Science Reviews* 76, 114–128.
- Pigati, J. S., McGeehin, J. P., Muhs, D. R., Grimley, D. A. & Nekola, J. C. 2015: Radiocarbon dating loess deposits in the Mississippi Valley using terrestrial gastropod shells (Polygyridae, Helicinidae, and Discidae). *Aeolian Research* 16, 25–33.
- Pigati, J. S., Quade, J., Shahanan, T. M. & Haynes, C. V. 2004: Radiocarbon dating of minute gastropods and new constraints on the timing of late Quaternary spring-discharge deposits in southern Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 204, 33–45.
- Pigati, J. S., Rech, J. A. & Nekola, J. C. 2010: Radiocarbon dating of small terrestrial gastropod shells in North America. *Quaternary Geochronology* 5, 519–532.
- Ponel, P., Guiter, F., Gandouin, E., Pailles, C., Rioual, P., Djamali, M., Andrieu-Ponel, V., Leydet, M., Van der Putten, N. & de Beaulieu, J.-L. 2016: Novel insights from coleopteran and pollen evidence into the Lateglacial/Holocene transition in Aubrac, French Massif Central. *Palaeogeography, Palaeoclimatology, Palaeoecology* 463, 83–102.
- Pons, A. & Reille, M. 1988: The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 66, 243–263.
- Preece, R. C. 1997: The spatial response of non-marine Mollusca to past climate changes. In Huntley, B., Cramer, W., Morgan, A. V., Prentice, H. C. & Allen, J. R. M. (eds.): *Past and Future Rapid Environmental Changes*, 163–177. Springer, Berlin & Heidelberg.
- Preece, R. C. & Bridgland, D. R. 1998: *Late Quaternary Environmental Change in North-West Europe: Excavations at Holywell Coombe, South-East England*. 425 pp. Springer, Dordrecht.
- Preece, R. C., Coxon, P. & Robinson, J. E. 1986: New biostratigraphic evidence of the Post-Glacial colonization of Ireland and for Mesolithic forest disturbance. *Journal of Biogeography* 13, 487–509.
- Puisségur, J.-J. 1976: *Mollusques continentaux quaternaires de Bourgogne*. 241 pp. Doin, Paris.
- Reimer, P. J. and 41 others 2020: The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62, 725–757.
- Renault, S., Forest, V., Magnin, F., Margarit, X., Mistrot, V., Thiébaud, S., Vigne, J.-D., Weydert, N. & Bourhis, J.-R. 1996: Les niveaux de l'Age du bronze du Mourre de la Barque à Jouques (Bouches-du-Rhône). Première analyse du mobilier et reconstitution paléoenvironnementale. *Documents d'Archéologie Méridionale* 19, 99–170.
- Roberts, N., Brayshaw, D., Kuzucuoğlu, C., Perez, R. & Sadori, L. 2011: The Mid-Holocene climatic transition in the Mediterranean: causes and consequences. *The Holocene* 21, 3–13.
- Roberts, N., Fyfe, R. M., Woodbridge, J., Gaillard, M.-J., Davis, B. A. S., Kaplan, J. O., Marquer, L., Mazier, F., Nielsen, A. B., Sugita, S., Trondman, A.-K. & Leydet, M. 2018: Europe's lost forests: a pollen-based synthesis for the last 11,000 years. *Scientific Reports* 8, 716, <https://doi.org/10.1038/s41598-017-18646-7>.
- Rousseau, D.-D. 1989: Réponses des malacofaunes terrestres quaternaires aux contraintes climatiques en Europe septentrionale. *Palaeogeography, Palaeoclimatology, Palaeoecology* 69, 113–124.
- Rousseau, D.-D. 1992: Is causal ecological biogeography a progressive research program? *Quaternary Science Reviews* 11, 593–601.
- Salvi, D., Harris, D. J., Kaliontzopoulou, A., Carretero, M. A. & Pinho, C. 2013: Persistence across Pleistocene ice ages in Mediterranean and extra-Mediterranean refugia: phylogeographic insights from the common wall lizard. *BMC Evolutionary Biology* 13, 147, <https://doi.org/10.1186/1471-2148-13-147>.
- Sánchez-García, C., Revelles, J., Burjachs, F., Euba, I., Expósito, I., Ibáñez, J., Schulte, L. & de Pablo, J. F.-L. 2024: What burned the forest? Wildfires, climate change and human activity in the Mesolithic–Neolithic transition in SE Iberian Peninsula. *Catena* 234, 107542, <https://doi.org/10.1016/j.catena.2023.107542>.
- Schmitt, T. & Varga, Z. 2012: Extra-Mediterranean refugia: the rule and not the exception? *Frontiers in Zoology* 9, 22, <https://doi.org/10.1186/1742-9994-9-22>.
- Stewart, J. R. & Lister, A. M. 2001: Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* 16, 608–613.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cosson, J.-F. 1998: Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7, 453–464.
- Ter Braak, C. J. & Smilauer, P. 2002: *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. www.canoco.com.
- Thiébaud, S. 1997: Early-Holocene vegetation and the human impact in central Provence (Var, France): charcoal analysis of the Baume de Fontbrégoua. *The Holocene* 7, 343–349.
- Thomas, K. D., Bell, M. & Limbrey, S. 1982: Neolithic enclosures and woodland habitats on the South Downs in Sussex, England. In Bell, M. & Limbrey, S. (eds.): *Archaeological Aspects of Woodland Ecology*, 147–170. BAR Publishing, Oxford.
- Triat-Laval, H. 1978: *Contribution pollenanalytique à l'histoire tardi- et postglaciaire de la végétation de la basse vallée du Rhône*. Ph.D. thesis, Université Paul Cézanne, 343 pp.
- Vialatte, A., Guiller, A., Bellido, A. & Madec, L. 2008: Phylogeography and historical demography of the Lusitanian snail *Elona quimperiana* reveal survival in unexpected separate glacial refugia. *BMC*

Evolutionary Biology 8, 339, <https://doi.org/10.1186/1471-2148-8-339>.

Welter-Schultes, F. W. 2012: *European Non-Marine Molluscs: A Guide for Species Identification = Bestimmungsbuch für europäische Land- Und Süßwassermollusken*. 679 pp. Planet Poster Editions, Göttingen.

Supporting Information

Additional Supporting Information to this article is available at <http://www.boreas.dk>.

Data S1. Summaries of malacological data using ordination diagrams. Comments to Figs S1–S3.

Fig. S1. MIR-1 La Stèle section. Detrended correspondence analysis (DCA). A = Species scatterplot; B = interpretation of the scatterplot; C = position of the molluscan assemblages on the scatterplot.

Fig. S2. MIR-5 Le Verger section. Correspondence analysis (CA). First biplot (left) and its interpretation (right). Only the most significant species are represented.

Fig. S3. La Thomassine section. Results of the correspondence analysis (CA). First biplot (left) and its interpretation (right). Only the most significant species are represented.

Table S1. Raw mollusc data from MIR-1 La Stèle.

Table S2. Raw mollusc data from MIR-5 Le Verger.

Table S3. Raw mollusc data from La Thomassine.

Table S4. Proposed ecological groups.