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The impact of Dansgaard–Oeschger cycles on the loessic environment and malacofauna of Nussloch (Germany) during the Upper Weichselian

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Abstract

A loess sequence has been sampled continuously at high resolution in Nussloch (Rhine Valley, Germany) for malacological and grain-size analyses between ca. 34 and 20 ka. Molluscan abundance and richness, percentage in hygrophilous species and grain-size index show cyclical variations related to the lithological loess–gley alternation. Major molluscan abundance maxima were triggered by temperature increases through an enhancement of the reproduction cycle, whereas cyclical richness fluctuations and percentage in hygrophilous species reflect variations in local humidity and changes in the environmental mosaic. Malacological parameters allow the distinction of four environmental phases organised in cyclical successions correlated with most of the loess–gley doublets. The correlation of the grain-size index of the Nussloch loess sequence with the dust content of the GRIP ice core demonstrates the synchronicity of major molluscan abundance maxima and $\delta^{18}O$ increases characterising temperature increases during Dansgaard–Oeschger interstades. A schematic model is proposed to link the North Atlantic Dansgaard–Oeschger climatic oscillations with local environmental changes indicated by both malacofauna and pedostratigraphy. This malacological study of the Nussloch loess sequence thus provides new information about the response of terrestrial loessic palaeoenvironments to millennial-timescale climatic fluctuations during the Upper Weichselian (~marine isotope stage 2 (MIS 2) and end of MIS 3).

Keywords: Terrestrial molluscs; Loess; Upper Pleistocene; Western Europe; Millennial-scale environmental changes; Dansgaard–Oeschger cycles

Introduction

The occurrence of millennial-timescale climatic changes was originally characterised by Dansgaard–Oeschger (D/O) cycles in Greenland ice-cores (Dansgaard et al., 1993), and Heinrich events (H) in North Atlantic sediments (Heinrich, 1988). Later, the study of numerous high-resolution oceanic, continental and ice records of both hemispheres refined their characterisation and the response of marine and terrestrial environments (see reviews by Voelker (2002) and Rohling et al. (2003). In Europe, the long records documenting millennial-timescale climatic and environmental changes that occurred during the last climatic cycle are the isotopic records of the Villars cave speleothem (Genty et al., 2003), and several terrestrial (Wijmstra, 1969; Woillard, 1978; Beaulieu (de) and Reille, 1984; Pons and Reille, 1988; Tzedakis, 1994; Reille and Beaulieu (de), 1995; Follieri et al., 1998; Müller et al., 2003; Tzedakis et al., 2004) and marine (Sanchez Goñi et al., 2000, 2002) palynological sequences. However, north of the Mediterranean domain, only the pollen record of the peat-bog cores of La Grande Pile (Franche-Comté, France) allowed the characterization of millennial-timescale continental environmental changes. Moreover, for the last glacial period, only the impact of the major climatic oscillations was recognized due to the limited time resolution of this record.

Conversely, during the last glaciation, the formation of loessic eolian deposits between the Scandinavian and Alpine ice sheets in Europe (Fink, 1969) was enhanced by the emerged and poorly vegetated shelves of the English Channel and the North Sea (Antoine et al., 2003; Bourillet et al., 2003; Van Huissteden and Pollard, 2003), and by the strong westerly atmospheric circulation (COHMAP Members, 1988; Renssen and Bogaart,

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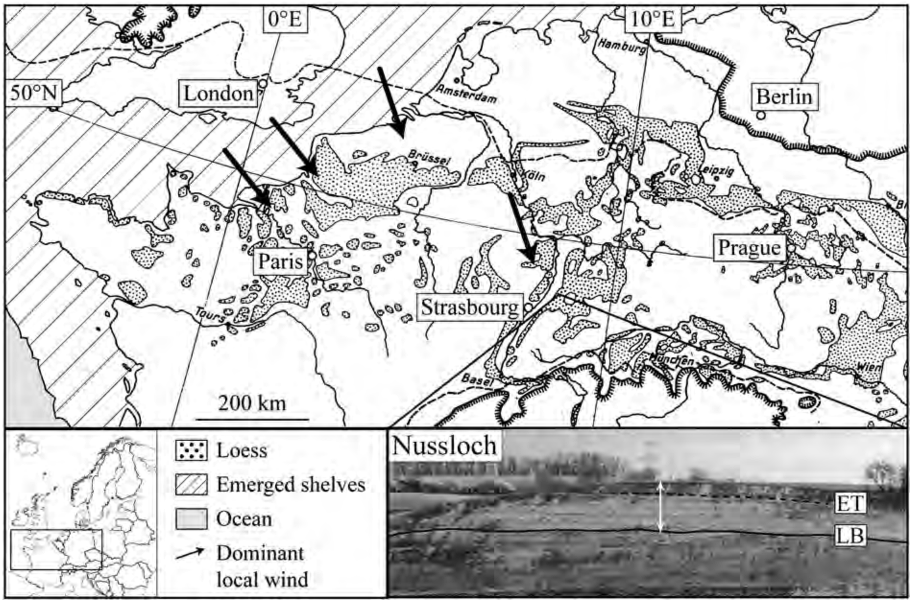

Figure 1. Location and picture of the Nussloch site. Loess deposits and maximum extension of ice-sheets during the last glacial maximum after Grahmann (1932). LB: Lohner Boden (soil); ET: Eltviller tuff. The white double-headed arrow represents about 15 m of sediment.

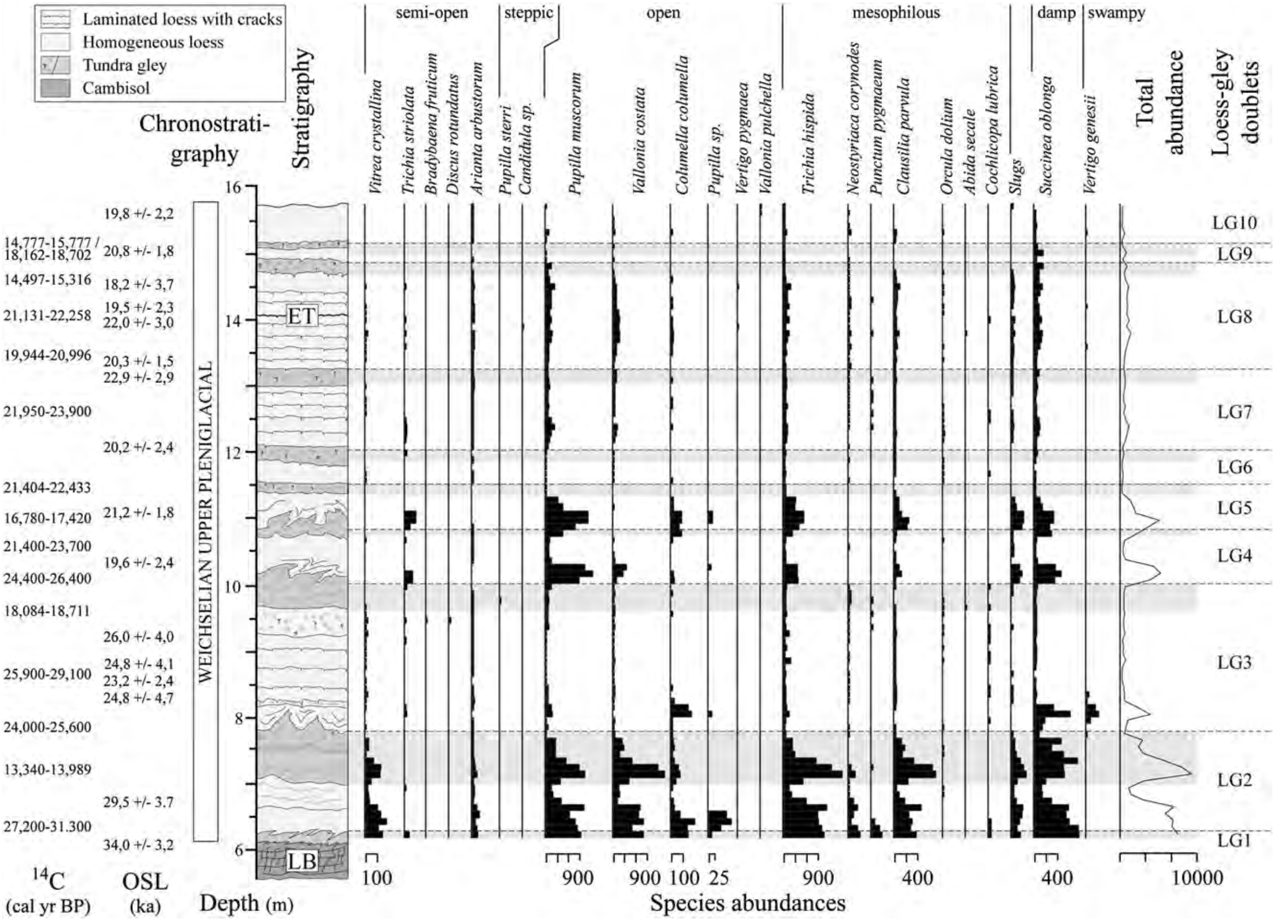

Figure 2. Upper Weichselian part of the Nussloch P3 sequence. Dating framework: Hatté et al. (2001b) for ^{14}C and Lang et al. (2003) for OSL. Chronostratigraphy and lithology modified from Antoine et al. (2001). ET: Eltviller Tephra; LB: Lohner Boden. Original species abundances are displayed with a square-root scale. Species are classified by habitat type. The ambiguous *Pupilla* shells have been put aside in a *Pupilla* sp. group.

2003). In these deposits, loess and gley (tundra soils) alternations were described in many loess sequences across Europe (Haesaerts, 1980; Haesaerts, 1985; Frechen et al., 1997; Antoine et al., 1999; Frechen, 1999; Frechen et al., 1999; Antoine et al., 2001), and those recently described in Nussloch (Rhine Valley, Germany: Fig. 1) were tentatively associated with Dansgaard–Oeschger events (Rousseau et al., 2002, 2007). Hatté et al. (1999, 2001a) and Hatté and Guiot (2005) reconstructed millennial-scale vegetation changes, and proposed paleoprecipitation reconstructions, for the last glaciation based on a geochemical analysis of the Nussloch loess organic matter. Besides, unlike pollen grains, which are often oxidised, large quantities of terrestrial mollusc shells are generally well-preserved in loess and allow precise palaeoenvironmental reconstructions (Ložek, 1964; Puisségur, 1976) for geographical areas and time spans for which the potential of pollen sequences and speleothems is limited.

The aim of this study is thus to detect and to characterise the millennial-timescale environmental variability throughout the Nussloch loess section by analysing molluscan populations and comparing them with sedimentological features. After the examination of the quality of the molluscan record, the discussion tackles the relationships between Nussloch mollusc populations and palaeoenvironmental parameters according to modern observations, and a schematic model is proposed to link malacological and pedostratigraphic changes to millennial-timescale climatic oscillations.

Materials and methods

The Nussloch quarries are located on the eastern flank of the Rhine Valley, ~10 km south of Heidelberg, Germany (Fig. 1). During the last glaciation, the site was equidistant from both Scandinavian and Alpine ice sheets and was directly influenced by the circulation and dynamics of the Westerlies. The studied section, labelled P3, is located in the middle of a *greda* or loess dune, oriented NNW–SSE and parallel to the local dominant wind direction (Léger, 1990; Antoine et al., 2001). The section is composed of a 9.5-m-thick alternation of nine loess and nine gley layers (Fig. 2). It is bracketed by the Lohner Boden (LB) at the base, which is considered as the last Middle Pleniglacial soil in southern Germany (Frechen, 1999), and by the Eltviller tuff (ET) near the top. Thermoluminescence ages for LB and ET are respectively 34,800 ± 370 yr (NU-7) and 22,100 ± (?) yr (NU-1) (Zöller et al., 1988). This time interval is also supported by IR-OSL (Lang et al., 2003) and ^{14}C-AMS (Hatté et al., 2001b) datings (Fig. 2). The close similarity of both P2 and P3 lithological records made easy to locate precisely in P3 all these datings performed throughout P2 (Antoine et al., 2002).

In addition to pedostratigraphic observations, grain-size analyses have been performed continuously every 10 cm, using a Coulter particle-size analyzer. The grain-size index (GSI), defined as the proportion of coarse silt (26 to 56.2 μm) divided by the proportion of fine silt plus clay (<26 μm), has been used to characterise fluctuations of the paleowind strength: the highest values indicate the windiest conditions (Porter and An, 1995; Vandenberghe et al., 1997; Rousseau et al., 2002). Parallel to grain-size samples, 95 loess samples of 10 L (about 10–15 kg) have been taken continuously every 10 cm for terrestrial mollusc analyses. Once washed and sieved at 0.42 mm, 63,497 individuals were identified (Table 1) and allocated to 22 species (Table 2) divided up in six ecological groups: semi-open, steppic, open, mesophilous, damp and swampy habitats (Ložek, 1964; Puisségur, 1976). Difficult to identify only with their internal shell, slugs have been considered as a single species for the calculation of ecological parameters of the malacofauna. The “slugs” group has been neglected in environmental interpretations as it may include species with different ecological requirements.

The richness (number of species) and both relative and absolute abundances (number of individuals) (Figs. 2 and 3) were calculated following the method of Ložek (1964). To avoid underestimations in individual counts of each species, the abundance is given by the number of complete shells plus the largest of unique shell parts (apices or apertures). When complete shells, apices and apertures are absent, five whorl fragments are considered to represent one individual. For larger species (diameter > 1 cm) an additional correction is applied to the estimation (Ložek, 1964).

A Juveniles/Adults (J/A) index has been calculated to characterise demographic changes triggered by environmental and/or climatic changes (Moine et al., 2005). As the differentiation between intact shells of juvenile individuals and broken shells of adult individuals without aperture is not always possible, the J/A ratio has been estimated on the basis of entire shells (E), apices (Ax), and apertures (Ap) for the tolerant and dominant species *Pupilla muscorum* (Fig. 3) present throughout the sequence:

$$\frac{J}{A} = \frac{Ax - Ap}{E + Ap}$$

A four-point running mean has also been calculated to smooth the artificial high frequency variability that low abundances may have induced (Fig. 3).

Finally, a millennial-timescale chronology has been established to correlate the Nussloch loess sequence with the GRIP ice core to look for relationships between molluscan populations, environmental changes and climatic fluctuations. However, errors of OSL datings and inversions in ^{14}C and OSL chronologies (Fig. 2) led us to choose the method developed by Rousseau et al. (2002) for the Nussloch loess profile P2 rather than that of Hatté et al. (2001a,b). The loess grain-size index and the GRIP dust record have thus been correlated using 12 tie-points associated with their major fluctuations (Fig. 4). Indeed, as the transportation and deposition of particles in both sites depended on the dynamics of the atmospheric polar cell during the last glaciation, both proxies are expected to show the same major variations (Rousseau et al., 2002, 2007). As all available dating methods for loess fail to measure the short duration of hiatuses that may have occurred at loess–gley transitions, the loess deposition was assumed to be continuous in first approximation.

Table 1
Molluscan counts per sample

Ecological groups		Semi-open					Steppic		Open						Mesophilous							Slugs	Damp	Swampy	Total	
Samples	Species	*Vitrea crystallina*	*Trichia striolata*	*Bradybaena fruticum*	*Discus rotundatus*	*Arianta arbustorum*	*Pupilla sterri*	*Candidula sp.*	*Pupilla muscorum*	*Vallonia costata*	*Columella columella*	*Pupilla sp.*	*Vertigo pygmaea*	*Vallonia pulchella*	*Trichia hispida*	*Neostyriaca corynodes*	*Punctum pygmaeum*	*Clausilia parvula*	*Orcula dolium*	*Abida secale*	*Cochlicopa lubrica*		*Succinea oblonga*	*Vertigo genesii*	*Individuals*	*Species*
15.6–15.7		0	0	0	0	1	0	0	1	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	6	5
15.5–15.6		0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	5	5
15.4–15.5		0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	1	0	5	4
15.3–15.4		0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	3	0	7	5
15.2–15.3		0	0	0	0	2	0	0	10	4	2	0	0	0	8	3	0	5	1	0	0	0	2	1	38	10
15.1–15.2		0	0	0	0	1	0	0	2	0	0	0	0	0	2	0	0	1	0	0	0	0	2	0	8	5
15.0–15.1		0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	9	0	11	3
14.9–15.0		0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	67	0	70	4
14.8–14.9		0	0	0	0	1	0	0	1	2	0	0	0	0	2	1	0	0	0	0	0	0	5	0	12	6
14.7–14.8		0	1	0	0	0	0	0	23	0	0	0	0	0	1	1	0	0	0	0	0	0	59	0	85	5
14.6–14.7		0	1	0	0	1	0	0	6	2	0	0	0	0	2	1	0	1	1	0	0	1	14	0	30	10
14.5–14.6		0	2	0	0	1	0	0	15	6	1	0	0	0	3	1	0	4	0	0	0	3	16	0	52	10
14.4–14.5		1	3	0	0	30	0	0	62	11	0	0	1	0	33	2	0	21	2	0	0	7	48	0	194	12
14.3–14.4		0	0	0	0	2	0	0	24	7	0	0	0	0	18	1	0	7	1	0	0	4	25	0	89	9
14.2–14.3		0	0	0	0	2	0	0	29	8	1	0	0	0	19	4	2	7	0	0	0	4	10	0	86	10
14.1–14.2		2	2	0	0	3	0	0	23	10	1	0	0	0	25	5	0	6	2	0	0	2	18	1	100	13
14.0–14.1		2	2	0	0	4	0	0	19	21	0	0	0	0	9	1	0	2	1	0	0	0	16	0	77	10
13.9–14.0		1	5	0	0	5	0	0	29	31	2	0	0	0	21	2	0	5	0	0	1	8	40	0	150	12
13.8–13.9		0	0	0	0	0	0	1	17	21	2	0	1	0	5	1	0	5	0	0	0	1	20	0	74	10
13.7–13.8		4	5	0	0	6	0	0	41	42	3	0	0	0	27	3	1	14	0	1	0	9	48	0	204	13
13.6–13.7		2	0	0	0	3	0	0	21	31	3	0	0	0	20	2	0	5	0	0	0	2	40	0	129	10
13.5–13.6		1	3	0	0	3	0	0	12	11	2	0	0	0	5	3	0	7	1	0	0	5	23	1	77	13
13.4–13.5		2	1	0	0	1	0	0	9	7	1	0	0	0	7	1	0	2	0	0	0	3	9	0	43	11
13.3–13.4		1	1	0	0	2	0	0	9	6	0	0	0	0	2	2	0	3	1	0	0	2	6	0	35	11
13.2–13.3		0	1	0	0	2	0	0	3	2	0	0	0	0	6	3	0	2	0	0	0	1	6	0	26	9
13.1–13.2		0	1	0	0	1	0	0	6	7	0	0	0	0	4	1	0	1	0	0	0	1	13	0	35	9
13.0–13.1		0	1	0	0	4	0	0	11	8	1	0	0	0	9	1	1	3	0	0	0	2	6	0	47	11
12.9–13.0		1	1	0	0	3	0	0	14	6	0	0	0	0	8	1	0	2	0	0	0	1	9	0	46	10
12.8–12.9		0	1	0	0	1	0	0	5	3	0	0	0	0	5	1	1	1	0	0	0	1	3	0	22	10
12.7–12.8		1	0	0	0	1	0	0	3	5	1	0	0	0	5	1	1	1	0	0	0	0	2	0	21	10
12.6–12.7		1	0	0	0	1	0	0	10	6	1	0	0	0	17	1	0	2	1	0	0	0	4	0	44	10
12.5–12.6		1	2	0	0	1	0	0	5	4	0	0	0	0	3	1	1	2	1	0	1	1	3	0	26	13
12.4–12.5		0	4	0	0	1	0	0	23	0	0	0	0	0	6	2	0	2	1	0	1	2	17	0	59	10
12.3–12.4		0	9	0	0	2	0	0	58	14	1	0	0	0	14	1	1	1	1	0	0	3	24	0	129	12
12.2–12.3		0	9	0	0	1	0	0	30	7	0	0	0	0	13	0	0	5	3	0	0	2	13	0	83	9
12.1–12.2		0	5	0	0	1	0	0	18	6	0	0	0	0	12	0	0	1	1	0	0	1	6	0	51	9
12.0–12.1		0	1	0	0	2	0	0	3	0	0	0	0	0	2	1	0	1	0	0	0	0	3	0	13	7
11.9–12.0		0	8	0	0	0	0	0	1	2	0	0	0	0	5	0	0	1	0	0	0	0	8	0	25	6
11.8–11.9		0	1	0	0	1	0	0	2	1	0	0	0	0	2	1	0	1	1	0	0	0	1	0	11	9
11.7–11.8		0	1	0	0	0	0	0	1	2	0	0	0	0	2	0	0	1	1	0	0	0	0	0	8	6
11.6–11.7		1	2	0	0	1	0	0	2	1	0	0	0	0	3	0	0	2	1	0	1	0	2	0	16	10
11.5–11.6		1	1	0	0	1	0	0	2	1	1	0	0	0	2	1	0	0	1	0	0	0	1	0	12	10
11.4–11.5		0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	0	0	0	0	1	0	7	3
11.3–11.4		0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	1	0	0	0	0	2	0	9	4
11.2–11.3		0	0	0	0	0	0	0	83	0	2	0	0	0	49	0	0	18	0	0	0	7	14	0	173	6
11.1–11.2		0	0	0	0	0	0	0	125	0	6	0	0	0	116	0	0	19	0	0	0	12	29	0	307	6
11.0–11.1		0	0	0	0	0	0	0	240	2	3	0	0	0	91	0	0	37	0	0	0	19	44	0	436	7

10.9–11.0	0	117	0	0	0	0	0	1481	0	76	16	0	0	336	0	0	159	0	0	0	127	280	0	2592	8
10.8–10.9	0	36	0	0	1	0	0	693	0	51	0	0	0	183	0	0	112	0	0	0	74	186	0	1336	8
10.7–10.8	0	14	0	0	1	0	0	90	0	76	0	0	0	61	0	0	3	0	0	0	2	217	0	464	8
10.6–10.7	1	5	0	0	1	0	0	14	1	2	0	0	0	5	0	0	1	1	0	0	2	4	0	37	11
10.5–10.6	0	0	0	0	1	0	0	10	0	0	0	0	0	1	1	0	0	0	0	0	3	1	0	17	6
10.4–10.5	0	0	0	0	1	0	0	9	1	0	0	0	0	3	0	0	1	0	0	0	3	2	0	20	7
10.3–10.4	0	2	0	0	1	0	0	26	6	0	0	0	0	5	0	0	1	0	0	0	0	10	0	51	7
10.2–10.3	0	0	0	0	0	0	0	1196	150	0	5	0	0	154	0	0	17	0	0	0	53	373	0	1948	7
10.1–10.2	0	61	0	0	0	0	0	1776	82	3	0	0	0	151	0	0	35	0	0	0	84	578	0	2770	8
10.0–10.1	0	58	0	0	0	0	0	910	12	7	0	0	0	162	0	0	1	0	0	0	51	340	0	1541	8
9.9–10.0	0	9	0	0	0	0	0	25	1	0	0	0	0	12	1	0	2	0	0	1	2	10	0	63	9
9.8–9.9	0	1	0	0	2	0	0	6	3	1	0	0	0	3	3	0	0	0	0	0	2	3	0	24	9
9.7–9.8	0	1	0	0	2	2	0	8	1	0	0	0	0	4	5	2	0	1	0	0	0	1	0	27	10
9.6–9.7	1	1	0	0	1	0	0	4	3	0	0	0	0	4	1	0	1	1	1	1	0	3	0	22	12
9.5–9.6	1	2	0	0	2	0	0	6	6	2	0	0	0	8	2	1	2	1	0	0	0	4	0	37	12
9.4–9.5	3	3	1	1	1	0	0	3	2	0	0	0	0	2	2	0	1	0	0	0	0	3	0	22	11
9.3–9.4	1	2	0	0	2	0	0	7	3	0	0	0	0	3	1	1	1	1	0	1	1	3	0	27	13
9.2–9.3	3	2	0	0	1	0	0	1	1	0	0	0	0	21	1	0	3	1	0	1	0	3	0	38	11
9.1–9.2	1	3	0	0	1	0	0	2	1	0	0	0	0	1	1	0	1	0	0	1	0	2	0	14	10
9.0–9.1	1	1	0	0	2	0	0	1	1	0	0	0	0	12	0	0	1	1	0	0	0	3	0	23	9
8.9–9.0	2	0	0	0	2	0	0	2	1	0	0	0	0	1	1	0	1	0	0	1	0	5	0	16	9
8.8–8.9	2	0	0	0	2	0	0	2	3	0	0	0	0	36	2	0	1	1	0	1	0	5	0	55	10
8.7–8.8	2	1	0	0	1	0	0	2	2	0	0	0	0	1	0	0	1	0	0	0	0	1	0	11	8
8.6–8.7	0	0	0	0	1	0	0	1	1	0	0	0	0	3	1	0	1	0	0	0	1	0	0	9	7
8.5–8.6	1	0	0	0	0	0	0	1	1	0	0	0	0	2	1	0	1	0	0	0	0	1	0	8	7
8.4–8.5	1	0	0	0	1	0	0	5	3	1	0	0	0	5	1	0	4	0	0	1	1	1	0	24	11
8.3–8.4	3	1	0	0	1	0	0	5	4	0	0	0	0	6	2	0	5	0	0	1	1	3	4	36	12
8.2–8.3	1	1	0	0	3	0	0	6	1	9	0	0	0	5	1	0	3	0	0	0	1	2	2	35	12
8.1–8.2	1	3	0	0	1	0	0	28	1	222	0	0	0	8	0	0	1	0	0	0	0	276	68	609	10
8.0–8.1	0	8	0	0	0	0	0	37	0	322	8	0	0	26	0	0	0	0	0	0	0	1035	117	1553	7
7.9–8.0	0	2	0	0	1	0	0	2	4	1	0	0	0	3	0	0	0	0	0	1	0	81	17	112	9
7.8–7.9	1	1	0	0	1	0	0	4	1	2	0	0	0	1	1	0	1	1	0	0	0	54	0	68	11
7.7–7.8	0	0	0	0	1	0	0	1	4	2	0	0	0	4	1	0	1	0	0	0	1	20	1	36	10
7.6–7.7	9	2	0	0	1	0	0	85	71	5	0	0	0	72	0	0	42	0	0	0	7	580	0	874	10
7.5–7.6	10	1	0	0	1	0	0	88	100	10	0	0	0	58	0	0	86	1	0	0	11	217	0	583	11
7.4–7.5	1	0	0	0	2	0	0	81	40	2	0	0	0	109	0	0	48	1	0	0	14	671	0	969	10
7.3–7.4	46	0	0	0	5	0	0	336	284	7	0	0	0	828	0	0	306	0	0	0	63	1445	0	3320	9
7.2–7.3	186	0	0	0	9	0	0	886	1593	33	0	0	0	1858	5	1	1151	0	0	0	129	676	0	6527	11
7.1–7.2	169	0	0	0	13	0	0	1212	2137	57	0	0	0	2739	40	0	1391	0	0	0	180	733	0	8671	10
7.0–7.1	27	0	0	0	1	0	0	179	188	18	0	0	0	289	1	0	147	0	0	0	28	110	0	988	10
6.9–7.0	5	3	0	0	3	0	0	22	24	2	0	0	0	26	1	0	6	1	0	0	3	34	0	130	12
6.8–6.9	7	0	0	0	3	0	0	45	36	0	0	0	0	43	2	0	15	1	0	0	5	45	0	202	10
6.7–6.8	14	0	0	0	1	0	0	188	17	6	0	0	0	385	17	0	73	0	0	0	16	213	0	930	10
6.6–6.7	124	0	0	0	18	0	0	1149	563	9	0	0	0	1427	60	0	574	0	0	0	98	886	0	4908	10
6.5–6.6	209	0	0	0	39	0	0	448	507	66	249	0	0	904	19	0	167	0	0	0	83	793	0	3484	11
6.4–6.5	345	0	0	0	12	0	0	670	726	426	386	0	0	956	6	12	245	0	0	3	50	941	0	4778	13
6.3–6.4	133	0	0	0	13	0	0	788	297	207	115	0	0	1163	71	48	190	0	0	4	25	1529	0	4583	13
6.2–6.3	227	23	0	0	25	0	0	931	703	212	8	0	0	1309	107	76	356	0	0	5	72	1634	0	5688	14

Results

Pedostratigraphy and sedimentology

The P3 sequence shows an alternation of loess and gley layers. Loess–gley transitions have been selected as stratigraphic limits as they results from a synchronous resumption of loess deposition, at least all over the site, after each stop or strong decrease of sedimentation during the formation of gleys. Conversely, lower gley boundaries could not be used as synchronous stratigraphic limits as their position depends on both local water availability and topography during the gley formation (Antoine et al., 2002; Moine et al., 2005). Ten loess–gley doublets (LG) have thus been distinguished: G1, LG2, up to L10 (Rousseau et al., 2002).

Besides, the curve of the grain-size index shows a saw-toothed pattern (Fig. 3). Minima occur in all gleys except G6 and G7 whereas higher values characterise loess, suggesting windier conditions during the loess deposition than during the gley formation (Antoine et al., 2002).

Quality of the molluscan record

A thorough check of shell preservation and assemblage homogeneity has been done to avoid biases in palaeoenvironmental interpretations, given the high sampling resolution.

Among the list of taphonomic processes that influenced the vertical distribution and the preservation of complete shells and fragments throughout a humic rendzina profile (Carter, 1990), we neglected the weak diagenetic processes of tundra soil formation, and the activity of ants (not detectable) and earthworms (only low abundances in earthworm calcium-carbonate granules). Soil movements, density changes and leaching more probably explain the shell fragmentation than predation by small mammals or birds, even for large species with diameters >1 cm more subject to predation. Given the similar size of most of the shells, and the presence of centimetric sedimentological structures, size-dependent sorting, mixing and burial processes did not affect the composition of shell assemblages. Moreover, the good preservation of the surface, the microsculpture and the edges of shells and fragments refutes the occurrence of shell transportation and chemical dissolution. This is also supported by the absence of artificial *post-mortem* accumulation of shells and by the higher average carbonate content ($CaCO_3=23.8\%$) in Nussloch than in other western European loess sequences (Antoine et al., 2001). Consequently each sample is considered to be homogeneous and formed by shell fractions of the same age, which supports, among others, the reliability of the calculation of the Juveniles/Adults ratio.

According to the dating framework, each sample represents an average time span of 100 to 200 yr. Even if it is typical in loess, the recovery of less than 250 individuals in many assemblages suggests either a very low density or a discontinuous presence of mollusc populations in the sampled zone, which might be due to winter soil frost, summer low temperatures and damp conditions rather than depleted vegetation given that the richness oscillates between 5 and 10 species.

Finally, concerning an eventual shift between the shells and the sediment, we must first note that, except a few burying species like *Cecilioides acicula*, most of them are living on the ground and do not bury more than 5 to 10 cm in depth to hatch or to hibernate. Cook (2001) only indicates that mortality affects

Table 2
Environmental characteristics of the modern species identified in the Nussloch P3 sequence, after (Germain, 1930; Adam, 1960; Likharev and Rammel'meier, 1962; Zilch and Jaeckel, 1962; Ložek, 1964; Kerney et al., 1983)

Abida secale (7)	Dry, sunny and hot stations with low vegetation, only in calcitic regions. Rarely in woody places	*Pupilla muscorum* (5)	Open, dry or weakly wet and sunny stations
Arianta arbustorum (2)	Very wet and vegetated stations. Cold-resistant. Also in open stations (humid meadows, alpine grasslands)	*Pupilla sterri* (4)	Very dry and sunny stations among calcitic rocks and fallen stones, and with a scarce vegetation
Bradybaena fruticum (2)	Wet and vegetated stations (woods, near rivers). Also in scrub and dry woodland. Mostly absent from open and sunny stations	*Succinea oblonga* (8)	Wet stations with a sparsed vegetation (humid meadows, swamps and near streams)
Clausilia parvula (7)	Mostly in dry open stations with calicitc rocks and low vegetation. Rare in woods	*Trichia hispida* (7)	Everywhere except driest stations
Cochlicopa lubrica (7)	Wet stations (woods, humid meadows, swamps)	*Trichia striolata* (2)	Wet and shaded stations with vegetation
Columella columella (5)	In cold regions and wet stations with herbaceous swamps, subarctic woods and grasslands	*Vallonia costata* (5)	In open, dry and humid, stations with stones. Rarely in woods or swamps
Discus rotundatus (2)	Varied, humid to dry, stations with a developed vegetation cover. Sometimes among rocks and fallen stones. Also present in open stations	*Vallonia pulchella* (5)	Humid and open habitat (wet and swampy meadows, near river banks and swamps). Mostly rare in dry meadows, and very rare in woods
Neostyriaca corynodes (7)	In stony meadows, and near mossy calcitic rocks. Sometimes in woody valleys near streams	*Vertigo genesii* (8)	In swampy stations (swamps, flooded meadows)
Orcula dolium (7)	Calcitic and fairly dry to wet stations (wood litter among rocks, slopes with loose stones)	*Vertigo pygmaea* (5)	Varied habitats prefering humid stations (wet and swampy meadows, near river banks) than dry and open ones
Punctum pygmaeum (7)	Varied. Fairly wet habitats with a developed vegetation cover (wood litter). Also in open stations if the humidity and protection against dehydration are adequate	*Vitrea crystallina* (2)	Cool and humid stations (woods, wet meadows, near swamps and streams)

Types of habitat: 2: semi-open, 4: steppic, 5: open, 7: mesophilous, 8: damp, 9: swampy (Puisségur, 1976).

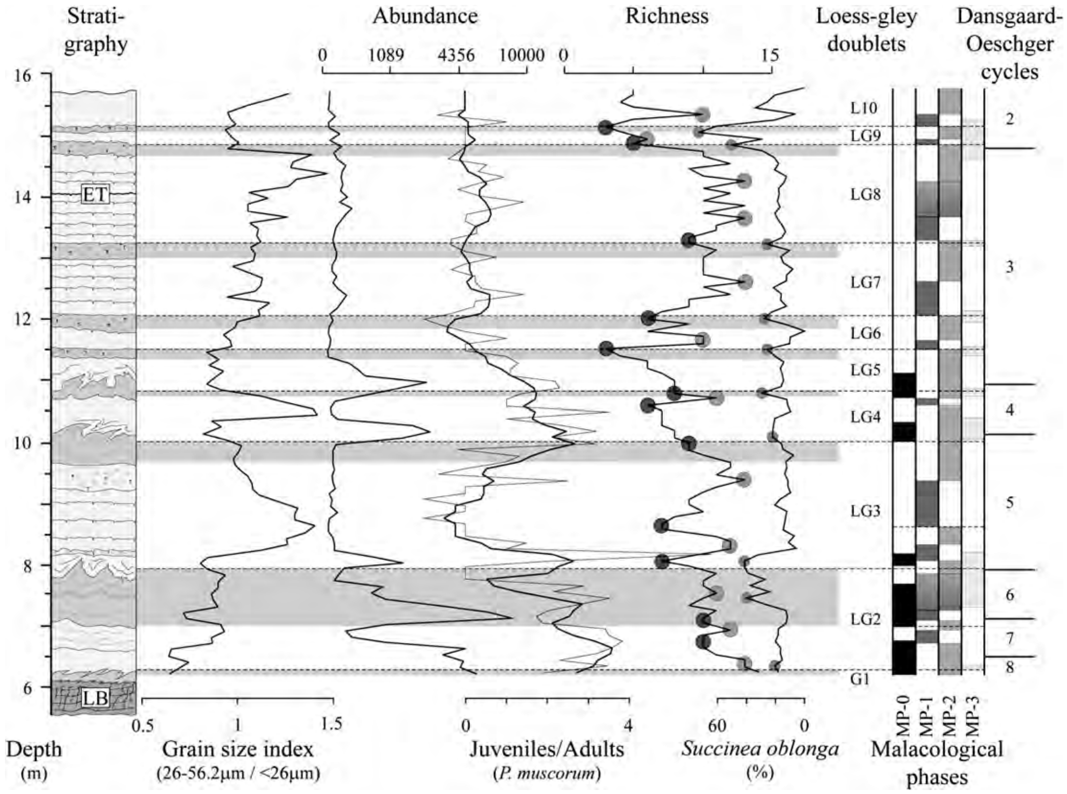

Figure 3. Sedimentology, parameters of the malacofauna and environmental phases. Abundance is displayed with a square root scale; Juveniles/Adults ratio (original (thin line) and smoothed (thick line) signals); richness minima and maxima are respectively underlined by dark grey and light grey circles in every LG doublets; grey circles also underlines maxima of *Succinea oblonga* relative frequencies. MP-0: high abundance; MP-1: increasing richness; MP-2: decreasing richness; MP-3: increases in *Succinea oblonga* relative frequencies above 20%. Legend of sedimentological features on Figure 2.

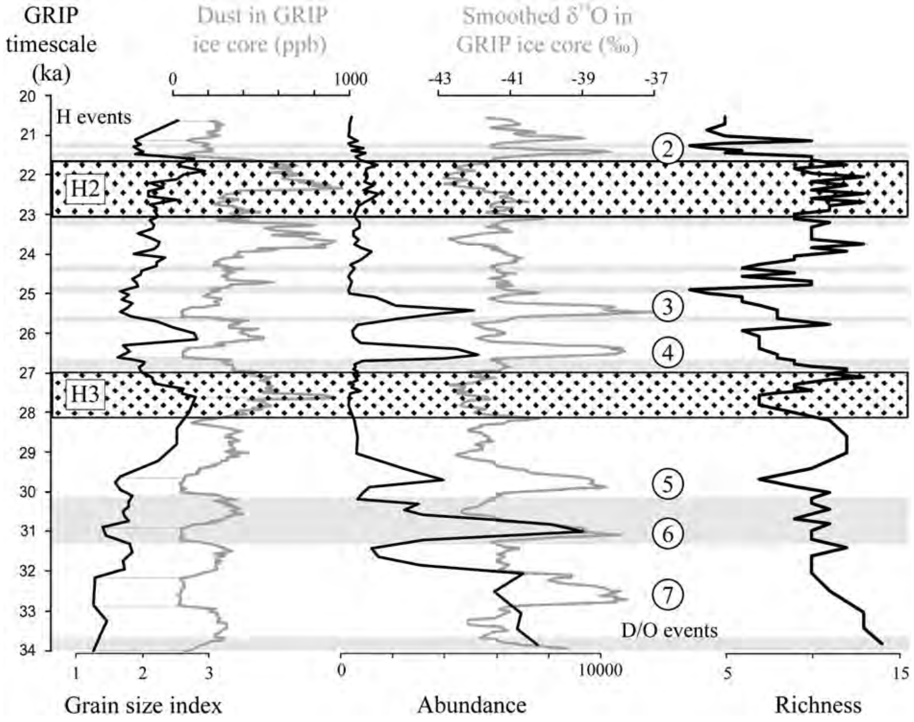

Figure 4. Correlation between Nussloch loess sequence and GRIP ice-core environmental proxies between ca. 34 and 20 ka. GRIP data: dust content (De Angelis et al., 1997); $\delta^{18}O$ (Dansgaard et al., 1993); chronology (Johnsen et al., 1997). Labelling of D/O events (Dansgaard–Oeschger interstades) and H events (Heinrich events) are respectively from Dansgaard et al. (1993) and Heinrich (1988). The $\delta^{18}O$ record smoothed with a four-point running mean to approximate the mollusc sampling resolution. The correlation has been performed with the software Analyseries (Paillard et al., 1996) using twelve reference points (horizontal segments).

eggs during hibernation and that hibernation quality and duration determine the longevity of individuals after the spring arousal. However, the presence of many empty shells on the ground in modern environments suggests that many adult molluscs die on the ground during their activity period. Consequently, without reliable estimates of winter mortality, and according to the average time span of samples and to the hibernation depth, we considered in first approximation that shells have the same age as their enclosing sediment.

Mollusc populations

Most of the species abundances show a similar pattern of variations that resembles that of total abundance (Fig. 2). The total abundance is generally less than 250 individuals per sample, except during five increases of different magnitude composed of three to six consecutive assemblages, each of which contains 500 to 10,000 individuals. These abundance increases are located at the top gleys G1, G2 (also at the base), G3, and G4, and they are synchronous with the lowest minima of the grain-size index (Fig. 3). Their total abundance and composition are also slightly different (Fig. 2). However, no abundance increases coincide with the grain-size index minimum around G8 and G9, and neither abundance increases nor grain-size index minima occur at the top of gleys G5, G6 and G7. The running mean of the *J*/*A* ratio varies between 0 and 4 and is positively correlated with abundance variations (Fig. 3). The relative frequency of the single damp habitat species *Succinea oblonga* (Table 2) shows a relationship with the lithological loess–gley alternation. Increases above 20% occurs at the top of gley units, often synchronously with minima or strong decreases in richness ($r = -0.19$; $p < 0.1$) and in relative frequencies of semi-open, open, and mesophilous ecological groups (Fig. 3).

The richness ranges between 3 and 14 species, which is common for European loess assemblages (Ložek, 1990; Rousseau et al., 1990), shows a regular saw-toothed pattern from LG6 to L10 with an increase at the base of each LG doublet followed by a decrease toward the top (Fig. 3). In the lower half of the sequence, the relationship with LG doublets is more complex and the previous richness variation cycle within LG doublets is modified as follows: a stable phase replaces the richness increase at the base of LG5. In LG4, the richness cycle is postponed in the upper part of the loess. LG3 includes two richness cycles. In LG2, a strong decrease in richness occurs first in the loess followed by two richness cycles of low amplitude, except the strong richness decrease at the top of the gley. Richness fluctuations are due to the discontinuous presence of vegetation-requiring species such as *Trichia striolata, Punctum pygmaeum, Vitrea crystallina, Arianta arbustorum, Discus rotundatus* and *Bradybaena fruticum*, hygrophilous species such, as *Vertigo genesii, Cochlicopa lubrica* and *Columella columella*, and to the sporadic presence of *Orcula dolium* and *Neostyriaca corynodes* (Table 2). Species appearances or disappearances are not ordered during richness increases and decreases. Finally, despite their relationships with the loess–gley alternation, richness and abundance fluctuations are not statistically correlated ($r = 0.21$; $p < 0.05$). Hence, both parameters will be first discussed separately before being included in a more general climatic and environmental schematic model.

Table 3
Life traits of the identified species in the Nussloch P3 sequence, after (Falkner et al., 2001)

	Species	Self fertilization	Eggs number	Eggs development time (weeks)	Maturity (yr)	Longevity (yr)
Dominant and strongly reacting species	*Clausilia parvula*	N	1–10	<2<	1<	2–5
	Columella columella	Not included in Falkner et al. compilation				
	Pupilla muscorum	Y>N	1–10	<2	1 and 1<	2–5
	Succinea oblonga	N	1–100	<2<	1 and 1<	1–2
	Trichia hispida	N	1–100	2<	1	2–5
	Trichia striolata	N>>Y	1–100	2<	1	2–5
	Vallonia costata	Y>>N	1–10	<2	<1	<1–2
Secondary and weakly reacting species	*Abida secale*	Y	1–10	<2	1	2–5
	Arianta arbustorum	N	1–100	2<	1<	5<
	Bradybaena fruticum	N	1–100	2<	1<	2–5
	Clausilia dubia	N	1–10	2<	1<	2–5
	Cochlicopa lubrica	Y>>N	1–10	<2	<1 and 1	1–5
	Discus rotundatus	Y=N	1–10	2<	1	1–2
	Neostyriaca corynodes	Not included in Falkner et al. compilation				
	Orcula dolium	Y=N	1–10	2<	1 and 1<	2–5
	Punctum pygmaeum	Y=N	1–10	2<	1	1–2
	Pupilla sterri	Y>N	1–10	<2	1 and 1<	2–5
	Vallonia pulchella	Y	1–100	<2	<1	<1–2
	Vertigo genesii	Y>>N	1–10	<2	<1	1–2
	Vertigo pygmaea	Y>N	1–10	<2	<1	1–2 (–5)
	Vitrea crystallina	Y>>N	1–10	2<	<1	1–2

Y = yes, N = no: in a single species both can occur in the same proportions (=) or one can dominate weakly (< or >) or strongly (<< or >>)
Candidula sp. has not been included as it groups presently three species in Europe, with different life traits values.

Discussion

Abundance

Origin of abundance increases

Chemical dissolution and artificial *post-mortem* accumulations of shells have been previously discarded. Increases in the shell concentration have been noted during fieldwork. The influence of loess grain-size variations occurring mainly below 0.2 mm (Antoine et al., 2001) on the concentration in complete shell and fragments (>0.42 mm) has been neglected. The number of individuals is on average 50 per assemblage in loess and more than 1500 during abundance increases. A four-time lower sedimentation rate during abundance increases would imply a seven-time longer shell accumulation if the density of the mollusc population was still constant. This basic estimate is not consistent with the chronological framework (Fig. 2) and cannot justify alone the molluscan abundance increases. Consequently, only the occurrence of growth phases of the mollusc population can explain such abundance increases, and expected associated demographic changes are supported by increases in the Juveniles/Adults ratio calculated for *Pupilla muscorum* (Fig. 3).

Environmental and biological influences on the abundance of modern malacofauna

First, the size of a mollusc population fluctuates yearly in response to environmental changes (Solem, 1984). Higher temperatures favour food assimilation and growth (Pelseneer, 1935; Chevallier, 1982), egg-laying and duration of the embryonic life (Pelseneer, 1935), egg development rate (Kerney et al., 1983), reduced time between mating and egg-laying, reduced time between two egg-laying periods (Pelseneer, 1935), and reduced mortality of early juveniles at the end of the egg-laying season (Pelseneer, 1935). A higher humidity influences egg-laying frequencies (Madec and Daguzan, 1987), fecundity, embryo development and egg hatching rate (Potts, 1975). Photoperiod also influences egg-laying (Ford and Cook, 1994). Altogether, terrestrial mollusc biology is thus primarily influenced by temperature and secondarily by humidity.

Second, to test the influence of species biological features, several life traits have been selected in the database of Falkner et al. (2001), and the values favouring the population growth have been underlined for each species present in Nussloch (Table 3). However, this does not separate either species showing strong increases during abundance maxima from the others, and it does not separate Nussloch species from others selected in the database. Indeed, self-fertilization is arbitrarily distributed among the terrestrial mollusc genus and species (Heller, 2001). The smaller the size of individuals and species, the lower is the number of eggs per clutch (Madec and Daguzan, 1987; Heller, 2001). Egg development time, maturity and longevity are strongly influenced by environmental parameters, especially temperature (Pelseneer, 1935; Uminski, 1975; Chevallier, 1982; Watabe, 1983; Baur, 1984; Daguzan and Le Guen, 1987; Gomot et al., 1987; Lambert and Daguzan, 1987). Moreover, the photoperiod influences metabolism and physiology of juvenile individuals of *Helix aspersa* (Aupinel and Daguzan, 1989), humidity influences haemolymph osmolality (Phifer and Prior, 1985) and concentration (Pelseneer, 1935; Riddle, 1983; Cook, 2001), and alimentation influences haemolymph calcium concentration (Langley, 1979). Environmental influences on physiology can differ from species to species, but in the end they determine the occurrence and length of activity periods, and thus the size of species populations.

Consequently, environmental parameters have a greater influence than life traits on species relative frequencies, which can be reliably interpreted in terms of palaeoenvironmental changes, as already concluded by Solem (1984) and Bengtsson and Baur (1993). The occurrence of centennial periods of warmer and favourable moisture conditions would have enhanced the reproduction cycle, favoured the survival and development of juveniles, and thus resulted in large increases in the mollusc abundance and *J*/*A* ratio. Differences in the magnitude of species increases within each peak would thus result from slight differences in environmental conditions.

A global/regional temperature forcing for molluscan abundance?

In absence of adequate regional high-resolution temperature records, we compared the mollusc abundance with the δ^{18}O signal from the GRIP ice core (Greenland), which mainly reflects atmospheric temperature changes. This comparison comes directly out from the correlation of the loess grain-size index with the ice dust content, as malacological and sedimentological proxies in Nussloch are synchronous. The mollusc abundance increases appear to be synchronous with those of the δ^{18}O (Fig. 4), which characterise interstades of Dansgaard–Oeschger (D/O) cycles and reflect temperature increases of about 8–12°C above Greenland between ca. 40 and 20 ka, and only 5–6°C during the smaller D/O event 2 (Masson-Delmotte et al., 2005). According to model outputs from Ganopolski and Rahmstorf (2001), mollusc population increases have been triggered by interstadial temperature increases that were maximal above the North Atlantic deep water formation area and eastward-decreasing across Europe. Their intensity rather depended on changes in the intensity of the thermohaline circulation (Broecker, 1994) and in the latitudinal position of the sea-ice limit and in the position of the storm track over Europe (Renssen and Bogaart, 2003). The absence of mollusc abundance increase at the top of gleys G8 and G9, synchronously with the strong grain-size index decrease (Figs. 3 and 4), may imply a too weak heat inflow over Europe during D/O 2, as suggested by the weaker temperature increase in GRIP and the strong negative anomaly in sea surface temperature of the moisture source area (Masson-Delmotte, 2005). In marine cores located west of the British and Norwegian coasts, both larger amounts of ice-rafted debris and higher percentages in the foraminifera species *Neogloboquadrina pachyderma sinistra* also indicate that sea surface temperatures were lower during D/O 2 than during other interstadials, as a result of the melting of huge amounts of icebergs generated during the cold Heinrich event 2 (Knutz et al., 2001; Rasmussen et al., 1997), synchronously with the minimum in the relative sea level (Lambeck et al., 2002). In addition, the shift of the δ^{13}C towards low values above the Eltviller tuff (Hatté et al., 1999), followed by high relative frequencies in *Succinea oblonga* throughout gleys G8 and G9, reflect a strong humidity increase, although associated paleo-precipitation reconstructions show either a decrease (transfer function) or no change (inverse modeling) (Hatté and Guiot, 2005).

However, it is not yet possible to push further the discussion by relating the magnitude of both abundance and temperature increases, as abundance increases are also influenced by cryoturbation and changes in the sedimentation rate and also depends on the number of identified species. Indeed, as almost all species abundances increase during D/O events, the more species there are, the larger the total abundance increase, provided no limiting factor, such as available food, restrains it (Fig. 3). However, contrary to the Lower and Middle Pleniglacial (Moine et al., 2005), the absence of species appearances during Upper Pleniglacial abundance increases is remarkable. Coope (2000) already suggested that climatic ameliorations during D/O events were not intense or long enough to modify considerably the vegetation composition. Most of the richness fluctuations occur during stadial phases, when loess is deposited, and the absence of recolonisation of the site area during Upper Pleniglacial interstades (Fig. 3) thus highlights their brevity and/or lower intensity and the more remote distance of refuges. However, the limited precision of dating methods and lacks in the knowledge of refuges and species dispersion speeds prevent further discussions about the timing of richness fluctuations, even if they underline longer and progressive environmental changes during stadial phases than during interstades.

Richness

At the top of gleys, minima in richness (Fig. 3) and in relative frequencies of species characterising open, semi-open, and mesophilous habitat indicate a decrease in the vegetation and in the habitat diversity. In the same time, maxima in relative frequencies of *Succinea oblonga*, minima in δ^{13}C of loess organic matter (Hatté et al., 1999) and characteristic sedimentological features of gleys (Antoine et al., 2001) imply the synchronous occurrence of moisture increases. Conversely, the co-dominance of the four main ecological groups (open, semi-open, mesophilous and damp habitat) synchronous with minimal relative frequencies of *Succinea oblonga* during richness maxima suggests a drier mosaic landscape with larger patches of vegetation during phases of loess deposition. Consequently, increases from low to high richness underline shifts from moister to drier and more vegetated environmental conditions, and reciprocally, but without significant changes in the general tundra-like environment.

Schematic model of environmental and climatic changes in Nussloch

The aim is now to schematise millennial-timescale environmental and climatic changes in Nussloch based on the variations of malacological and sedimentological parameters and to relate them with Dansgaard–Oeschger cycles and/or Heinrich events. In the following discussion, the terms “winter” and “summer” will be used to deal with the cold and warm seasons, respectively.

Malacological/environmental phases

According to previous discussions, the environment in Nussloch oscillated between drier and more vegetated conditions (MP-1 phase: trend in increasing richness), and more humid and less vegetated conditions (MP-2 phase: trend in decreasing richness) during all the Upper Pleniglacial (Fig. 3). Only two transition zones characterised by a relatively constant richness in LG2 and LG8 suggest that general environmental conditions remained particularly stable in Nussloch during D/O 6 and Heinrich event 2 (Figs. 3 and 4). As long as the sedimentation rate is considered constant, some MP-1 phases seem to be shorter than MP-2 ones. The constant proportion (10–20%) of *Succinea oblonga* (damp habitat) indicates that the local environment remained moist when the malacofauna was the most active.

Furthermore, during most of the moistest phases around the end of MP-2 phases, this proportion quickly and momentarily increased above 20% (MP-3 phase) (Fig. 3), whereas those of *Pupilla muscorum*, *Neostyriaca corynodes, Orcula dolium* and *Clausilia parvula* (dry and/or vegetated places) (Table 2) decrease. Increases in moist areas in the environmental mosaic, or moister periods particularly favourable to *Succinea oblonga* during the activity period, can thus rapidly take place. Generally short, these abrupt environmental changes (MP-3 phases), may last a longer time as in G2 and around LG9. There are two absences in L2 and in L3, and percentage increases in the middle of L3 and L10 are not considered as reliable MP-3 phases due to the very low abundance in shells.

The high molluscan abundances (MP-0 phase), implying summer temperature increases, occur in the lower half of the sequence. However, the high mortality rate in juveniles may result from a strong and rapid temperature decrease during summer-to-winter transitions, which prevent lately born snails to reach the required degree of growth to hibernate. We note here that above G1, the persistence of abundant population during loess L2 is clear, whereas it may be at least partly artificial and result from cryoturbation of gley tops at the base of loess L3, L4 and L5 (Fig. 5). MP-0 phases precede MP-1/MP-2/MP-3 successions. In LG4, this succession is postponed, whereas MP-1 lacks in LG5. Warmer periods would thus also

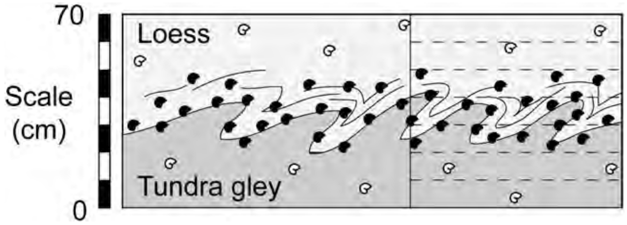

Figure 5. Artificial thickening of a mollusc abundance increase (black shells) in horizontal samples (dashed lines) close to an undulated loess–gley boundary (cryoturbation and or solifluction).

take place at MP-2/MP-1 transition and accompanied the beginning of the trend toward a drier and more vegetated environment.

Relationships with D/O cycles

According to the correlation framework established with Greenland climatic proxies (Fig. 4), MP-0 phases are, from the base to the top, associated with D/O events 7, 6, 5, 4, and 3, respectively. The correlation also suggests that the basal abundance peak was also triggered by the end of D/O event 8. The distribution of MP phases shows that D/O cycles 7, 6 and 4 are associated with a single MP-0/MP-1/MP-2/MP-3 succession, whereas others may include several environmental successions that occurred during a single stadial phase. The occurrence of MP-0 phases suggests that some of the climatic changes accompanying MP-2/MP-1 transitions might have been stronger than others and triggered temperature increases in addition to local moisture increases (MP-3 phases). As D/O cycles 7, 6 and 4 include each nothing less than a single MP-0/MP-1/MP-2/MP-3 environmental succession, each environmental succession may be triggered by a stadial–interstadial-like climatic cycle that may not always end by the occurrence of full interstadial conditions in Nussloch. On the opposite, abundance and relative frequency in *Succinea oblonga* do not reflect particular differences between environmental successions when full stadial conditions (highest aridity) are reached at each MP-1/MP-2 transition. However, according to diversity and equitability index values (Moine et al., 2002), the malacofauna is poorer and the species distribution is less homogeneous for MP-1/MP-2 transitions located in L2 (just above G1), G2, L4, L5 and L9, which all succeed to a P-0 phase, except that in L9 that is nevertheless associated D/O event 2. The proportion in moist areas in the environmental mosaic may have been higher during these stadial phases.

Relationships with sedimentological features

MP-0 phases, and more generally interstadial phases, are synchronous with low loess grain-size index (GSI) values (Fig. 4), which imply weaker wind strength than during other environmental and climatic phases. MP-0 phases occur at loess–gley transitions affected by cryoturbation (Fig. 3). Temperature increases during interstadial phases probably induced a rapid thaw of the permafrost and at the same time molluscan abundance increases. Indeed, most of the sequence is constituted by laminated loess with cryo-desiccation cracks especially marked in L3, L7 and L8. The freeze–thaw fabric of this so-called "niveo-eolian" loess indicates that seasonal freezing accompanied its deposition (Antoine et al., 2001). The permanent local moisture indicated by 10–20% in *Succinea oblonga* may thus result from the thawing of segregated soil ice or snow in summer. Moreover, the protection against low winter temperatures provided by the winter snow cover may have favoured the persistence of tundra-like vegetation and high molluscan richness in summer, even during stadial phases.

MP-3 phases are synchronous with gleys (Fig. 3), which are generally characterised by leaching and downward redistribution of carbonates and iron (Van Vliet-Lanoë, 1985). The MP-3 phase associated with gley G3 is slightly shifted above, however, but the increasing trend in *Succinea oblonga* relative frequency took place throughout G3. The thickest gleys are associated with the longest MP-3 phases. The formation of gleys implies important moisture increases while temperature remained cold, which is coherent with increases in *Succinea oblonga* relative frequencies, with a clear change in the aspect of the environmental mosaic, and with low molluscan abundances. During the Upper Pleniglacial, Nussloch was close to the limit between the continuous and discontinuous permafrost domains (Huijzer and Vandenberghe, 1998). Residual permafrost tables and well-developed ice wedges were described in loess sequences from northern France (Lautridou and Sommé, 1974; Antoine et al., 1999), Belgium (Haesaerts et al., 1981; Frechen et al., 2001) or The Netherlands (Vandenberghe et al., 1987; Vandenberghe and Van Huissteden, 1989). Their absence in Nussloch implies drier conditions due to lower precipitations and/or to the particular location of the sequence at the top of a greda on the Odenwald plateau. The higher density of root tracks and biological activity in gleys noted by Vandenberghe et al. (1998) and Antoine et al. (2001) seems contradictory with the vegetation decline inferred from richness minima, unless both occurred synchronously with abundance and/or richness increases postdating the formation of gleys.

The cycles of environmental successions are thus consistent with the loess–gley alternation, as one LG doublet is associated with one environmental succession, except LG2 and LG3. However, the absence of both gley formation and MP-3 phase suggest that the additional shift toward moister conditions occurring at the base of LG3 remained limited. The strong synchronous GSI increase suggests the occurrence of a particular atmospheric change. In LG2, the MP-3 phase also lacks at the transition between environmental successions of D/O 7 and D/O 6, but it is not evident whether gley formation should be considered as absent or merged at the basis of the thick gley G2, as P4 loess profile shows a two-folded gley G2 (Antoine et al., 2002). At the base of L2, the persistence of the MP-0 phase and the weak GSI increase within loess deposits suggest that the climate did not completely shift toward stadial conditions. However, the synchronous decreases in richness and in relative frequencies of vegetation-requiring species like *Punctum pygmaeum*, *Cochlicopa lubrica* and others well-represented in the Middle Pleniglacial deposits (Moine et al., 2005), underlines the Weichselian Middle-to-Upper Pleniglacial climatic transition (roughly MIS 3/2).

Consequently, changes in sedimentological features show that both sediment and malacofauna synchronously responded to high-resolution climatic fluctuations, and support some of the environmental interpretations based on the malacofauna.

Conclusion

The multi-proxy analysis of the Nussloch P3 loess sequence (Rhine Valley, Germany), including malacology, pedostratigraphy and grain-size analysis, provides a high-resolution record of local and cyclical palaeoenvironmental changes for the

Upper Weichselian (~marine isotope stage 2 (MIS 2) and end of MIS 3). The general parameters of the malacofauna (abundance and richness), the proportion in hygrophilous species, the grain-size index and the lithological loess–gley alternation have been correlated with global millennial-timescale climatic changes (Dansgaard–Oeschger (D/O) cycles 7 to 2 and Heinrich events H3 and H2) recorded in the GRIP ice core (Greenland) between ca. 34 and 20 ka. The loess sequence of Nussloch yields one of the most precise terrestrial records of palaeoenvironmental changes triggered by millennial-timescale climatic changes for the Upper Weichselian in the European Great Plain, north of the network of pollen-based palaeoenvironmental sequences.

A schematic model is proposed to describe the influence of global millennial-scale climatic changes on the malacofauna, the sedimentation, and the local environment through the definition of a succession of environmental phases and their relationships with stadial and interstadial phases. The results show the strong influence of D/O-like cycles and the ability of malacofauna to reflect temperature, moisture and vegetation changes during the Upper Weichselian. In contrast, the impact of Heinrich events on the malacofauna cannot be directly identified and needs the correlation with GRIP, or precise and adequate datings, to be discussed. In addition, according to the correlation method we chose, the higher number of environmental successions than that of D/O cycles during the Upper Weichselian suggests that mid-latitude areas may have been more sensitive to North Atlantic area climatic fluctuations than polar areas.

The characterisation of millennial-scale climatic changes in the European Great Plain has to be continued through malacological and sedimentological analyses of loess sequences to constrain more precisely the geographical extension and the importance of their impact on the environment, and to refine the proposed schematic model. The confirmed presence of loess–gley alternations within loess deposits across the European loess belt, from France to Ukraine (Fink, 1969) favours this prospective. Higher-resolution studies and the development of new dating methods will also be necessary to improve the timing of millennial-scale environmental changes and their correlation with triggering climatic oscillations.

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