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Paleoclimatic implications of the spatial patterns of modern and LGM European land-snail shell $\delta^{18}O$

Natalie M. Kehrwald [a,*], William D. McCoy [b], Jeanne Thibeault [c], Stephen J. Burns [b], Eric A. Oches [d]

[a] University of Venice, IDPA-CNR, Calle Larga S. Marta 2137, I-30123 Venice, Italy
[b] Department of Geosciences, University of Massachusetts, Amherst, MA 01003, USA
[c] Department of Geography, University of Connecticut, Storrs, CT 06269, USA
[d] Department of Natural and Applied Sciences, Bentley University, Waltham, MA 02452, USA

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ABSTRACT

The oxygen isotopic composition of land-snail shells may provide insight into the source region and trajectory of precipitation. Last glacial maximum (LGM) gastropod shells were sampled from loess from Belgium to Serbia and modern land-snail shells both record $\delta^{18}O$ values between 0‰ and −5‰. There are significant differences in mean fossil shell $\delta^{18}O$ between sites but not among genera at a single location. Therefore, we group $\delta^{18}O$ values from different genera together to map the spatial distribution of $\delta^{18}O$ in shell carbonate. Shell $\delta^{18}O$ values reflect the spatial variation in the isotopic composition of precipitation and incorporate the snails' preferential sampling of precipitation during the warm season. Modern shell $\delta^{18}O$ decreases in Europe along a N–S gradient from the North Sea inland toward the Alps. Modern observed data of isotopes in precipitation (GNIP) demonstrate a similar trend for low-altitude sites. LGM shell $\delta^{18}O$ data show a different gradient with $\delta^{18}O$ declining toward the ENE, implying a mid-Atlantic source due to increased sea ice and a possible southern displacement of the westerly jet stream. Balkan LGM samples show the influence of a Mediterranean source, with $\delta^{18}O$ values decreasing northward.

Introduction

Understanding the spatial variability in the isotopic composition of European precipitation during the last glacial maximum (LGM) may be useful in discerning the linkages between many climate subsystems. During the last glacial period, Europe was subject to large climate changes that influenced the ocean–atmosphere exchange of water and energy including fluctuations in sea level, ice volume, and radiation balance. These changes are reconstructed using climate proxies including ice cores, speleothems, and lake sediments. Here, we present the use of land-snail whole shell samples as a paleoclimatic indicator across low-elevation western and central Europe to examine differences between the spatial distribution of oxygen isotopes in precipitation between the LGM and today.

The LGM is defined by the EPILOG project (Environmental Processes of the Ice Age: Land, Oceans, Glaciers) as the interval between 19,000 and 23,000 cal yr BP (Mix et al., 2001). The LGM is an extreme but transient climate period that is relatively well-constrained by proxy data. Pollen data (Guiot et al., 2000; Peyron et al., 2005), paleoenvironmental reconstructions from beetles (Guiot et al., 1993), and gemorphological evidence (Dawson, 1992; Frenzel et al., 1992) have been used to estimate that winter temperatures were at least 13–20 °C lower than at present in eastern Europe and the Mediterranean regions. Models (HadCM3, MRI-CGCM1, and ECBILTCLIO) depict a summer cooling of 3–6 °C across most of western and central Europe (Kageyama et al., 2006). The LGM was drier than present throughout most of Europe, with moderate drying in the Mediterranean region and more pronounced aridity in the northern latitudes (Peyron et al., 1998; Ganopolsksi and Rahmstorf, 2001). Foraminifera-based reconstructions (Kucera et al., 2005) and models (Kageyama et al., 2006) suggest that LGM winter sea-ice extent could have reached 50°N in the North Atlantic, thereby influencing potential sources of water vapor. This article maps the trajectories of water vapor inland across Europe during the LGM using pulmonate gastropods as a proxy for precipitation-bearing masses.

The oxygen isotope composition of land-snail shells (Yapp, 1979; Lécolle, 1985; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005; Colonese et al., 2007) and snail-shell assemblages (Ložek, 1972; Goodfriend, 1992; Balakrishnan et al., 2005) have both been used to reconstruct regional environmental conditions and past climate. Oxygen isotope composition is expressed in δ-notation, where the value of measured ^{18}O to ^{16}O is calculated as:

$$\delta^{18}O = [(R_{sample} / R_{standard}) - 1] \times 1000‰$$

* Corresponding author. IDPA-CNR, Istituto per la Dinamica dei Processi Ambientali – Consiglio Nazionale delle Ricerche, Calle Larga Santa Marta 2137, I-30123, Venice, Italy. Fax: +39 041 234 8628.
E-mail address: Kehrwald@unive.it (N.M. Kehrwald).

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where $R = {}^{18}O/{}^{16}O$ is relative to the (Vienna) PeeDee Belemnite (VPDB) standard or (Vienna) standard mean ocean water (VSMOW) (Craig, 1957, 1961). The $\delta^{18}O$ of land-snail carbonate follows the geographic distribution of $\delta^{18}O$ in precipitation (Lécolle, 1985; Goodfriend, 1992; Yanes et al., 2009), although local factors such as water vapor (Goodfriend et al., 1989) and relative humidity (Balakrishnan and Yapp, 2004) may influence the shell $\delta^{18}O$ in arid conditions. Land snails are widely distributed in the Central European loess–paleosol sequences and incorporate the ${}^{18}O/{}^{16}O$ signature of meteoric water into their shell carbonate (Goodfriend, 1992; Balakrishnan et al., 2005), thus providing detailed oxygen isotope data over an extensive area. The lifetime of an average European land snail is 3–5 yr (Kerney et al., 1987), and each shell therefore represents a discrete time interval. Fossil gastropods can be collected from a general period as determined through radiocarbon dating of the shell carbonate, dating the sediments surrounding snail-shell samples using luminescence techniques such as thermoluminescence (TL) or infrared stimulated luminescence (IRSL) and/or aminostratigraphic correlations (Oches and McCoy, 1995a; Frechen, 1999; Rousseau et al., 2002). The loess itself contains information about regional atmospheric circulation and climatic conditions (Pye, 1995) and supplements any data derived from land-snail carbonate.

The relationship between the $\delta^{18}O$ of meteoric water and the $\delta^{18}O$ values of land-snail shells has been studied for over 30 years (Yapp, 1979; Magaritz et al., 1981; Lécolle, 1985; Goodfriend, 1991, 1992; Balakrishnan and Yapp, 2004; Yanes et al., 2009). Simple flux-balance models comparing predicted shell $\delta^{18}O$ values with published measurements of shell $\delta^{18}O$ demonstrate that variations in land-snail shell $\delta^{18}O$ is a function of temperature, relative humidity, $\delta^{18}O$ of water vapor, and $\delta^{18}O$ of liquid water ingested by the snail (Lécolle, 1985; Balakrishnan and Yapp, 2004). The climate information derived from land-snail shell $\delta^{18}O$ is dependent upon times of snail activity (Balakrishnan et al., 2005). The similarity between fossil and modern shell $\delta^{18}O$ is ascribed to the fact that the snails are only active during comparable environmental conditions (Colonese et al., 2007).

Snails are most active during and after a rain event and incorporate this rainwater into the formation of their shell aragonite (Ward and Slowtow, 1992). Although rainwater is the main source of water for pulmonate gastropods, the $\delta^{18}O$ composition of land-snail shells may be influenced by the $\delta^{18}O$ of dew in arid regions (Yapp, 1979; Goodfriend et al., 1989). However, in humid regions such as western continental Europe, precipitation and atmospheric water vapor exist in isotopic equilibrium. The dew that the snails drink is therefore a record of the oxygen isotope composition of local rainfall (Lécolle 1985; Goodfriend et al., 1989; Zanchetta et al., 2005; Yanes et al., 2009). High relative humidity has a negligible effect on snail body fluid $\delta^{18}O$, and as a result, the $\delta^{18}O$ of precipitation in lowland European sites may have more influence on the isotopic composition of land-snail shell carbonate than the $\delta^{18}O$ of water vapor or $\delta^{18}O$ of dew (Magaritz et al., 1981, Goodfriend et al., 1989). The amount of rainfall can also influence the $\delta^{18}O$ of precipitation, where increased rainfall results in depleted oxygen isotope values. This amount effect is primarily an issue in tropical ocean islands or locations receiving the majority of their annual precipitation from monsoon systems (Dansgaard, 1964; Rozanski et al., 1993) and is not expected to be a primary factor influencing the $\delta^{18}O$ of European land-snail shells. When rain-bearing masses move inland from the coast, their precipitation becomes increasingly negative with increasing distance from the water vapor source. This continental effect is evident in observational records of $\delta^{18}O$ in precipitation across the study area (Rozanski et al., 1993) and therefore affects the oxygen isotope values of the available water that the land snails incorporate into their aragonite structure. High-elevation sites have relatively negative $\delta^{18}O$ in precipitation (Dansgaard, 1964; Araguas-Araguas et al., 2000), and

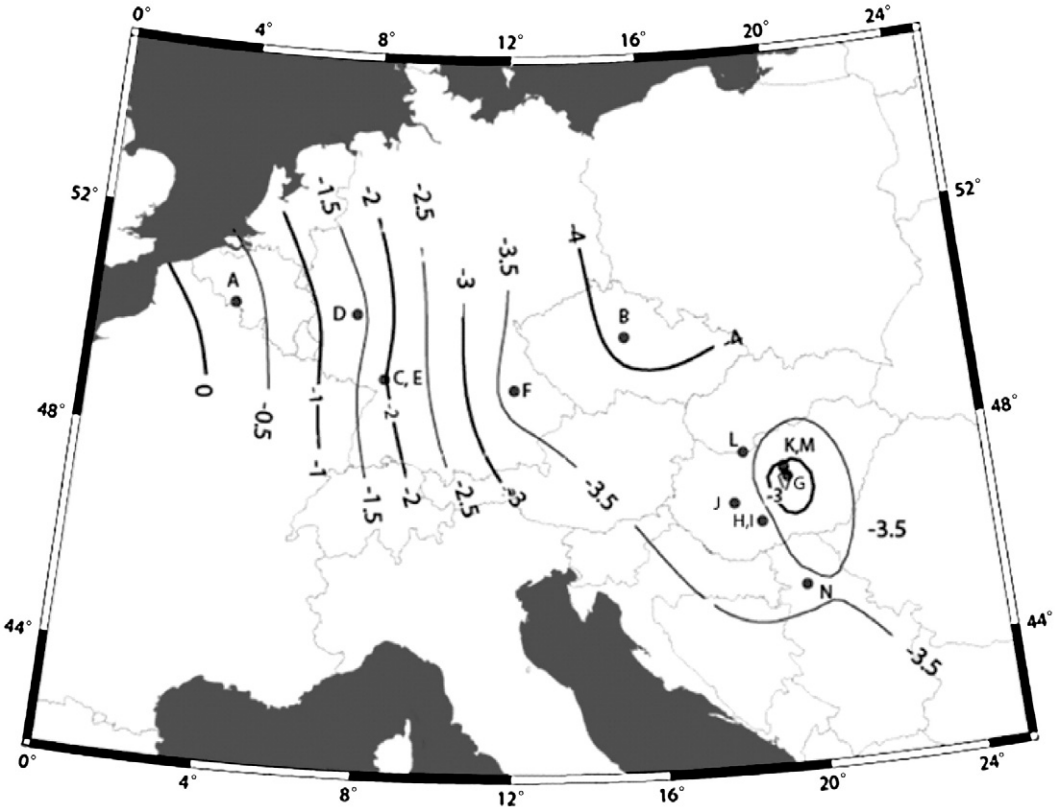

Figure 1. LGM sample sites. Spatial distribution of $\delta^{18}O$ of LGM land-snail shell carbonate. Oxygen isotope values were gridded using the Generic Mapping Tool's (GMT) geostatistical interpolator. Contours are every 0.5‰ (VPDB).

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Table 1
Fossil sample sites and coordinates in alphabetical order by country and site.

Site	Country	Locality	Latitude (°N)	Longitude (°E)	Altitude (m)	Sample age (ka)	Age error (ka)	Samples (*n*)	Genera	$\delta^{18}O$ (‰) for all genera	SD	Year	Dating method
A	Belgium	Harmignies	50.42	4.00	51	22.5	1.5	8	*Succinea*	0.39 to −0.51	0.31	2001	TL, IRSL, stratigraphic correlation, paleosols (Frechen et al., 2001)
B	Czech Republic	Kutná Hora	49.97	15.29	220	21.9	2.2	16	*Pupilla* *Succinea*	−2.96 to −5.44	0.66	2001	Aminostratigraphy (Oches and McCoy, 1995a); IRSL (Frechen et al., 1999)
C	Germany	Boeckingen	49.12	9.18	160	18.1 20.2	1.9 2.8	25	*Succinea*	−1.95 to −2.85	0.22	2002	Aminostratigraphy and marker soil horizons (Oches et al., 2000) TL (Zöller and Wagner, 1990)
D	Germany	Koblenz-Metternich	50.36	7.55	159	18	1	7	*Pupilla* *Succinea* *Trichea*	−1.45 to −2.26	0.30	2001	Tephra, marker loess and other stratigraphic correlation, IRSL (Boenick and Frechen, 2001)
E	Germany	Nussloch	49.32	8.71	213	19.2 19.6	1.7 2.4	26 30	*Succinea* *Trichea*	−1.69 to −2.38 −1.72 to −2.79	0.32	1993 2001	OSL, TL/IR, ^{14}C of wood and fossils, AMS of organic matter (Hatté et al., 1988; Zöller et al., 1988; Lösceher and Zöller, 2001; Rousseau et al., 2002)
F	Germany	Regensburg	49.03	12.12	332	~20	NA	15	*Succinea*	−2.84 to −3.57	0.40	1987	Cation exchange chromatography (W. McCoy personal communication)TL and stratigraphic correlation (Buch and Zöller, 1990)
G	Hungary	Albertirsa	47.25	19.62	108	19.2	2.2	14	*Pupilla* *Succinea*	−1.60 to −3.55	0.62	2002	IRSL, stratigraphic correlation (Stevens, 2003)
H	Hungary	Bátaszék	46.18	18.73	130	~20	NA	8	*Trichea*	−1.55 to −2.57	0.35	1987	Aminostratigraphy, paleosol correlation (Oches and McCoy, 1995a)
I	Hungary	Paks	46.47	18.83	130	~20	NA	13	*Trichea*	−3.30 to −4.60	0.36	1987	Tephra and paleosol correlation (Pésci, 1979; Oches and McCoy, 1995b)
J	Hungary	Ságvár	46.83	18.12	150	~20	NA	8	*Succinea*	−3.11 to −4.48	0.53	2002	Stratigraphic correlation (Stevens, 2003)
K	Hungary	Sulysap	47.45	19.53	185	~20	NA	38	*Trichea*	−1.66 to −3.64	0.63	2002	Aminostratigraphy, paleosol correlation (Stevens, 2003)
L	Hungary	Süttö	47.75	18.45	210	~20	NA	31	*Pupilla*	−2.60 to −4.21	0.61	2002	Aminostratigraphy; stratigraphic paleosol correlation (Oches and McCoy, 1995b; Stevens, 2003)
M	Hungary	Úri	47.42	19.53	168	~20	NA	30	*Pupilla* *Trichea*	−1.50 to −7.17	1.48	2002	Stratigraphic correlation (chernozem transition) (Stevens, 2003)
N	Serbia	Petrovaradin	45.25	19.88	85	~20	NA	14	*Pupilla* *Trichea*	−2.40 to −3.84	0.22	2002	Stratigraphic correlation (Stevens, 2003)

to address the influence of altitude on $\delta^{18}O$, only low-elevation sites (<400 masl) were used in this study.

Temperature also affects times of snail activity. Modern European land snails aestivate at temperatures above 27 °C and hibernate or become inactive at temperatures below 10 °C (Thompson and Cheny, 1996). The modern shells were collected in areas where the winter temperatures are sufficiently cold and the snails hibernate, with the exception of the sample site at Harmignies, Belgium. This selection process provides a control so that the modern snails are only sampling warm-season precipitation (Lécolle, 1985; Zanchetta et al., 2005). The LGM warm season was certainly much shorter than the modern warm season, but all LGM samples could only possibly be sampling warm-season precipitation due to the much lower LGM winter temperatures. Recent studies of the oxygen isotopic composition of land-snail shells suggest that shell $\delta^{18}O$ values serve as an indicator of $\delta^{18}O$ of warm-season precipitation (Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005), thereby taking into account the relatively higher $\delta^{18}O$ values of summer rainfall.

The direct influence of temperature on the $\delta^{18}O$ composition of the shells also complicates climate interpretations. The modern European precipitation–temperature relationship of the oxygen isotopic composition of precipitation represents an increase of 0.64‰ ± 0.04‰/°C increase and is calculated as 0.59‰/°C for the Last Glacial–Holocene transition (Rozanski et al., 1993). The aragonite–water system paleotemperature equation of Grossman and Ku (1986) for samples measured on the PDB scale is as follows: T (°C) = 21.8 − 4.69 ($\delta^{18}O_{argonite} - \delta^{18}O_{water}$). If snails are actively depositing shell material throughout the year, it is possible to use the mean annual temperature to calculate the fractionation between shell aragonite and snail body water. Modern continental European land snails are only active during a temperature range of 10–27 °C (Thompson and Cheny, 1996), and LGM snails can only possibly sample warm-season precipitation, thereby complicating the application of the aragonite–water system equation. However, observational studies where snails are active year-round (Yanes et al., 2009) and flux balance models (Balakrishnan and Yapp, 2004) demonstrate that, although the aragonite–water fractionation is modified by processes such as evaporation, the use of $\delta^{18}O_{shell}$ is a reliable proxy for $\delta^{18}O_{rain}$. The strong spatial coherence of $\delta^{18}O$ in precipitation across Europe at given time slices (Rozanski et al., 1993) allows for the analysis of the spatial variability of oxygen isotopes. In this article, we do not seek to compare the difference between modern and LGM $\delta^{18}O$ in mollusks, but rather to compare the spatial patterns of $\delta^{18}O$ between the two periods.

This study assesses the variability of oxygen isotopic composition in modern and LGM continental European land snails. After the factors of temperature, precipitation, seasonality, and/or changes in the source region and trajectory of rain-bearing masses are taken into account, time-slice maps are created from modern and LGM land-snail $\delta^{18}O$. Land-snail shells provide a means of evaluating the past distribution of

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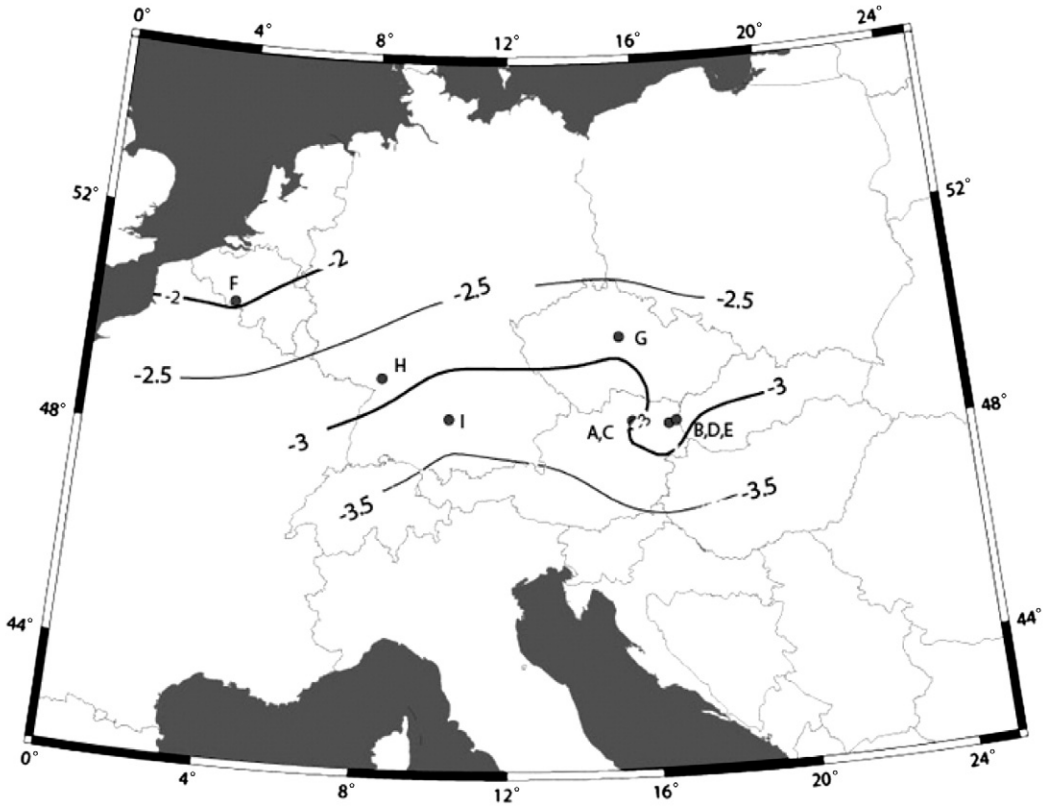

Figure 2. Modern sample sites. Spatial distribution of isotopic composition of modern land-snail carbonate. Modern genera include *Bradybaena*, *Cepea*, *Helicondonta*, *Helicopsis*, *Helix*, *Trichia*, and *Zebrina*. The oxygen isotope values were gridded using the Generic Mapping Tool's (GMT) geostatistical interpolator. Contours are every 0.5‰ (VPDB).

oxygen isotopes across much of the European continent and can add to the regional synthesis of European paleoclimate during the LGM.

Methods

Sample sites and selection of genera

All modern and fossil snail samples were gathered from Central European sites at elevations below 400 masl to facilitate dating and to control for altitude effects on the oxygen isotopic composition of the shells. LGM gastropods (*Pupilla*, *Succinea*, and *Trichia*) were gathered from sites in Belgium, Germany, the Czech Republic, Hungary, and Serbia (Fig. 1 and Table 1). LGM loess deposits have been previously dated using radiocarbon analyses, thermoluminescence (TL) techniques, or through aminostratigraphic correlations (Frechen, 1999; Oches and McCoy, 1995a). On a regional scale, the thickness of LGM loess sequences changes substantially, and the combination of amino-acid values, luminescence dates, and radiocarbon dates provides the most accurate method of correlating deposits. Each sample was dated by as many methods as possible (Table 1). Some samples at a single site were clearly separated by thousands of years, and in such a case, only the samples that were thought to be dated within the EPILOG LGM definition of 18 ka to 23 ka were used in this study. However, for samples that are dated by using previously published section

Table 2
Modern sample locations in alphabetical order by country and site.

Site	Country	Town	Latitude (°N)	Longitude (°E)	Altitude (masl)	Sample age (ka)	Age error (ka)	Samples (*n*)	Genera	$\delta^{18}O$ (‰) for all genera	SD	Year collected
A	Austria	Furth-Hohlweg	48.35	15.62	240	0	NA	55	*Cepea Helicopsis Zebrina*	−2.17 to −3.57	0.49	2003
B	Austria	Huhnertal	48.55	16.07	260	0	NA	5	*Bradybaena*	−4.31	0.00	2003
C	Austria	Krems	48.42	15.59	290	0	NA	75	*Bradybaena Cepea Helicopsis Zebrina*	−2.34 to −4.16	0.53	2003
D	Austria	Stillfried	48.40	16.83	165	0	NA	30	*Cepea*	−2.06 to −3.60	0.55	2003
E	Austria	Wolfstal	48.55	16.08	264	0	NA	45	*Bradybaena Cepea Helicopsis Helix*	−2.15 to −4.83	0.95	2003
F	Belgium	Harmignies	50.42	4.00	51	0	NA	10	*Trichea*	−1.14 to −2.42	0.71	2003
G	Czech Republic	Kutna Horá	49.97	15.29	220	0	NA	70	*Bradybaena Helicopsis Helix*	−2.02 to −4.39	0.79	2003
H	Germany	Nussloch	49.19	8.42	213	0	NA	20	*Helicondonta*	−2.30 to −3.20	0.50	2003
I	Germany	Offingen	48.48	10.37	440	0	NA	10	*Bradybaena*	−3.42 to −3.61	0.13	2003

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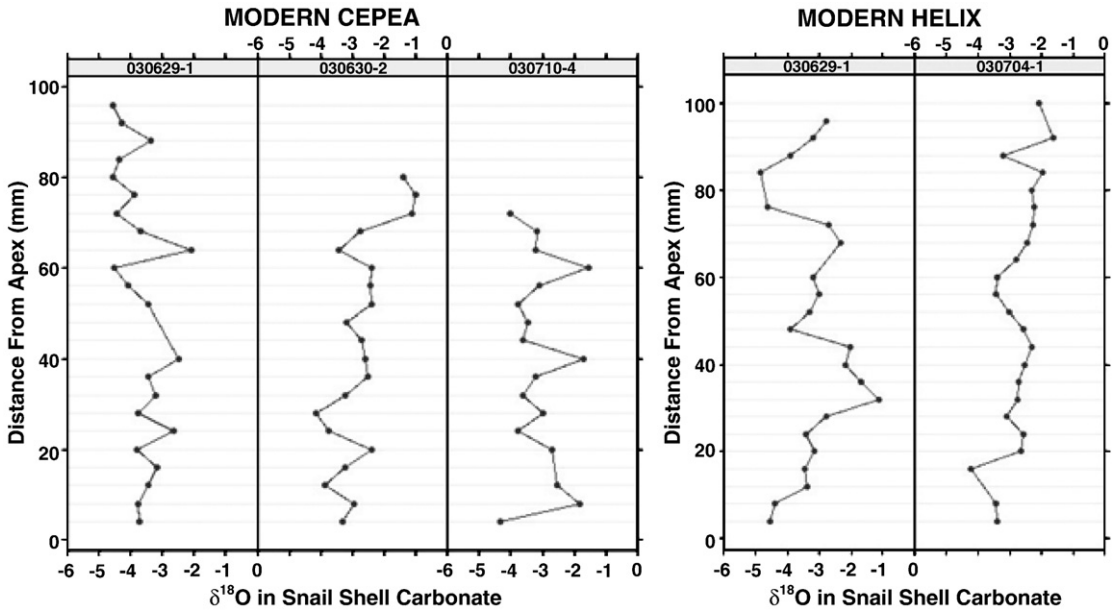

Figure 3. Variation (δ^{18}O VVPDB) within single modern *Cepea* and *Helix* shells. Samples were measured at 5-mm increments from the apex. The shells are differentiated by field number.

descriptions (Pésci, 1979; Oches and McCoy, 1995a; Oches et al., 2000; Frechen et al., 2001; Lösceher and Zöller, 2001; Rousseau et al., 2002; and Stevens, 2003), such precise dating and associated error are often not possible. The research is designed to incorporate a broad geographic extent, but the inclusion of disparate exposures decreases the precision of the time scale. Therefore, the term LGM should be thought of broadly, where included land-snail shells are older than 18 ka and are within stratigraphy corresponding to marine oxygen isotope stage 2 (MIS 2). All LGM shells retained the color and layered structure of their shells, including an intact nacreous layer on the inner layer, and none of the fossil shells had a chalky appearance. These factors suggest that the shells were not subject to postdepositional alteration.

Modern samples (*Bradybaena*, *Cepea*, *Helicodonta*, *Helicopsis*, *Helix*, *Trichea*, and *Zebrina*) were collected from the surface near many of the LGM sites and provided a control for comparison with fossil shell carbonate δ^{18}O (Fig. 2 and Table 2). These genera currently live in a variety of central European microclimates ranging from subarctic alpine conditions (*Trichea*) to damp woodlands (*Bradybaena*, *Cepea*, *Helicondonta*, *Helix*, and *Trichea*) to dry open areas (*Helicopsis*). *Helix* species are ubiquitous throughout Europe because they are cultivated for food and often escape their domestic environment (Kerney et al., 1987). Where possible, the same genera of modern and fossil shells were collected at an individual location.

Laboratory preparation

Carbonate isotopes were measured at the University of Massachusetts at Amherst using a Thermo-Finnegan Deltaplus mass spectrometer with a Kiel automated carbonate extraction device. Shell samples were cleansed by repeated rinsing and sonification and were dried overnight in a laboratory oven at 60 °C. Shells were drilled using a 0.5-mm carbide dental burr. This method does not preferentially sample only one shell layer but instead includes all layers of the shell aragonite. Fossil and modern shells of each genus at each site were sampled with the following methods: 1) sampling at the first, third, and fifth whorls; 2) crushed whole shell samples; and 3) crushed samples of five entire shells from a single genus and location. Three separate samples of the mixture of five crushed shells were prepared for measurement in the mass spectrometer. The internal standard of error for δ^{18}O analysis is $\pm$0.1‰. Only whole shell samples were compared with other whole shell samples to include any internal variability within shells. Arithmetic mean oxygen isotope values were calculated for each genus at each sample site.

Results and discussion

Measured variability in shell δ^{18}O

Within-shell, within-genus, within-site variability, between-genera, and between-site variability of the oxygen isotopic composition of land-snail shells were systematically analyzed to examine the validity of comparing shell δ^{18}O from different sites or ages. Land-snail δ^{18}O can vary by as much as 4‰ within a single shell (Fig. 3), although the majority of modern and LGM shells vary by only 2‰. The modern and fossil snail shells do not display a consistent trend of becoming increasingly enriched or depleted in oxygen isotopes with distance from the apex. Both modern and LGM within-shell values range between 0‰ and −5.5‰ The variability within shells is greater than or equal to the variability between shells. Henceforth, all discussions involve crushed whole shells that average the large intra-shell variations.

LGM land-snail shell δ^{18}O does not vary significantly between genera as shown by a two-way analysis of variance (two-way ANOVA) of LGM shell collections (Table 3). However, δ^{18}O does vary significantly by site, suggesting that snails are reflecting the spatial distribution of oxygen isotopes (Lécolle, 1985; Zanchetta et al., 2005). Fossil genera are therefore grouped together for spatial analysis of shell δ^{18}O.

The collection of only one modern genus at many sites increases the difficulty of separating differences between genera from differences by site. Other studies examining multiple mollusk genera have generally found no significant differences in δ^{18}O between modern genera

Table 3
Two-way analysis of variance (ANOVA) between LGM genera and LGM sites. The land-snail genus and site are treated as independent variables, while Genus: Site is the interaction between the genus and site factors, *df* = degrees of freedom, SS = sum of squares, MS = mean of squares.

	df	SS	MS	*F*	PF (>*F*)
Genus	4	5.168	1.292	1.6813	0.1516
Site	12	156.873	13.073	17.0136	$<2e-16$
Genus: Site	8	8.851	1.106	1.4400	0.1834
Residuals	185	142.149	0.768		

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Table 4
One-way analysis of variance (ANOVA) of modern shell $\delta^{18}O$ by site. *df* = degrees of freedom, SS = sum of squares, MS = mean of squares.

	df	SS	MS	*F*	PF (>*F*)
Site	8	9.9327	1.2416	2.7441	0.01269
Residuals	55	25.8853	0.4525		

(Lécolle, 1985; Zanchetta et al., 2005; Colonese et al., 2007; Yanes et al., 2009). For example, Lécolle (1985) asserts that there is little to no variation by genus for the modern genera used in our study (*Bradybaena*, *Cepea*, *Helicodonta*, *Helicopsis*, *Helix*, *Trichea*, and *Zebrina*), so it is likely that the variation that does occur represents variation by site and year-to-year variation in $\delta^{18}O$ in local rainfall. Zanchetta et al. (2005) and Colonese et al. (2007) argue that there is no conclusive proof that modern shell $\delta^{18}O$ differs significantly by species in Italy once isotopic variability due to altitude or aridity is taken into account. Studies attempting to determine if metabolic fractionation effects differ between genera report no definite changes in vital effects between species, meaning that between-genera changes in the oxygen isotopic composition of land-snail shells is not a function of the genera themselves, but rather a function of site (Lécolle, 1985; Goodfriend and Ellis, 2002). A one-way ANOVA of the collected modern shells shows significant differences between sites (Table 4), suggesting that with no evidence for variation between species, the shell aragonite records the spatial distribution of $\delta^{18}O$. Note that even shells in single collections did not grow in identical time periods, and thus, some variation is due to annual- to century-scale variation in $\delta^{18}O$ in precipitation even at a single location.

Our results are comparable to $\delta^{18}O$ measured in other low-elevation (<400 masl) European land-snail shells (Table 5), although all other studies have measured land-snail shells on the perimeter of the continent, which are primarily influenced by their proximity to oceanic sources of water vapor and which therefore have $\delta^{18}O$ near zero. Of the measured genera in this study, only two genera (*Cepea* and *Helix*) are the same as those measured by other studies. The range of measured $\delta^{18}O$ in *Cepea* is −2.16‰ to −3.60‰, while Cepea shells collected in France and Italy (Table 5) comprise a $\delta^{18}O$ of −0.10‰ to −1.69‰ (Lécolle and Letolle, 1990; Zanchetta et al., 2005). Modern *Helix* in this study has a range of −2.20‰ to −3.09‰, while more coastal locations have $\delta^{18}O$ values in the range of −0.91‰ to −2.50‰ (Zanchetta et al., 2005).

This study comprises the first continental-scale study of $\delta^{18}O$ in LGM land snails, and so there are few data with which to compare our results. The oxygen isotopic composition of fossil *Cepea* in the United Kingdom (UK) has a measured range of −1.15‰ to −1.67‰, where the fossil shells are not ascribed specific ages but are defined by their depth in the surrounding sediment (Yates et al., 2002). Late Pliocene Helix shells from central Italy have an oxygen isotopic range of −0.91‰ to −1.93‰ (Leone et al., 2000). Although these shells are closer to the ocean and are much older than the LGM samples measured in this study, the range of isotopic values lies within the measured fossil values of *Pupilla* (−1.45‰ to −7.17‰), *Succinea* (0.39‰ to −4.48‰), and *Trichea* (−1.55‰ to −4.89‰).

Comparison between spatial distribution of $\delta^{18}O$ in modern land-snail shells and GNIP data

It is necessary to compare the modern shell record with observational data to determine to what extent land-snail shell $\delta^{18}O$ records spatial changes in the isotopic composition of precipitation. The Global Network of Isotopes in Precipitation (GNIP) is a primary international resource of observational records. GNIP is a joint effort

Table 5
Oxygen isotopic composition of low-altitude European land-snail shells from other studies. These shells are all from the perimeter of the continent with a primarily maritime water vapor source and are not subject to the depletion of $\delta^{18}O$ due to the continentality effect. All dating of the fossil shells is described in their corresponding reference.

Country	Locality	Altitude (masl)	Age	Genera	$\delta^{18}O$ (‰)	References
France	Vienne en Arthies	95	Holocene	*Cepea*	−1.90	Lécolle and Létolle, 1990
France	Vernon	27	Holocene	*Cepea*	−1.50	Lécolle and Létolle, 1990
Italy	I. Martana	215	Modern	*Helix*	−0.10	Zanchetta et al., 2005
Italy	Chieti	550	Modern	*Helix*	−1.80	Zanchetta et al., 2005
Italy	Chieti	550	Modern	*Cepea*	−0.80	Zanchetta et al., 2005
Italy	Rome	40	Modern	*Cepea*	−0.60	Zanchetta et al., 2005
Italy	Tarquinia	200	Modern	*Cepea*	−1.40	Zanchetta et al., 2005
Italy	Velletri	500	Modern	*Helix*	−1.00	Zanchetta et al., 2005
Italy	Velletri	500	Modern	*Cepea*	−0.50	Zanchetta et al., 2005
Italy	Cancello	40	Modern	*Cepea*	0.70	Zanchetta et al., 2005
Italy	Trapani	150	Modern	*Cepea*	−0.10	Zanchetta et al., 2005
Italy	Seravezza	50	Modern	*Helix*	−1.00	Zanchetta et al., 2005
Italy	Cipollaiao 1	200	Modern	*Helix*	−1.30	Zanchetta et al., 2005
Italy	Cipollaio 4	500	Modern	*Helix*	−2.50	Zanchetta et al., 2005
Italy	Cipollaio 4	500	Modern	*Cepea*	−1.80	Zanchetta et al., 2005
Italy	Todi (Toppetti Quarry)	N/A	Late Pliocene	*Helix*	−1.79	Leone et al., 2000
Italy	Todi (Toppetti Quarry)	N/A	Late Pliocene	*Helix*	−0.91	Leone et al., 2000
Italy	Todi (Toppetti Quarry)	N/A	Late Pliocene	*Helix*	−1.93	Leone et al., 2000
UK	Oldlands Wood	N/A	Modern	*Helix*	−1.71	Yates et al., 2002
UK	Oldlands Wood	N/A	Modern	*Cepea*	−1.47	Yates et al., 2002
UK	Oldlands Wood	N/A	Modern	*Cepea*	−1.69	Yates et al., 2002
UK	Hayle Towans	N/A	Modern	*Cepea*	−0.40	Yates et al., 2002
UK	Graffy	N/A	Modern	*Cepea*	−1.35	Yates et al., 2002
UK	Caerwys	N/A	Fossil	*Cepea*	−1.67	Yates et al., 2002
UK	Caerwys	N/A	Fossil	*Cepea*	−1.64	Yates et al., 2002
UK	CBT	N/A	Fossil	*Cepea*	−1.40	Yates et al., 2002
UK	CBT	N/A	Fossil	*Cepea*	−1.60	Yates et al., 2002
UK	CBM	N/A	Fossil	*Cepea*	−1.15	Yates et al., 2002
UK	CBM	N/A	Fossil	*Cepea*	−1.32	Yates et al., 2002
UK	CBB	N/A	Fossil	*Cepea*	−1.65	Yates et al., 2002
UK	CBB	N/A	Fossil	*Cepea*	−1.54	Yates et al., 2002
UK	Newlands Cross	N/A	Fossil	*Cepea*	−1.23	Yates et al., 2002
UK	Newlands Cross	N/A	Fossil	*Cepea*	−1.30	Yates et al., 2002
UK	Castlethorpe	N/A	Fossil	*Cepea*	−1.53	Yates et al., 2002

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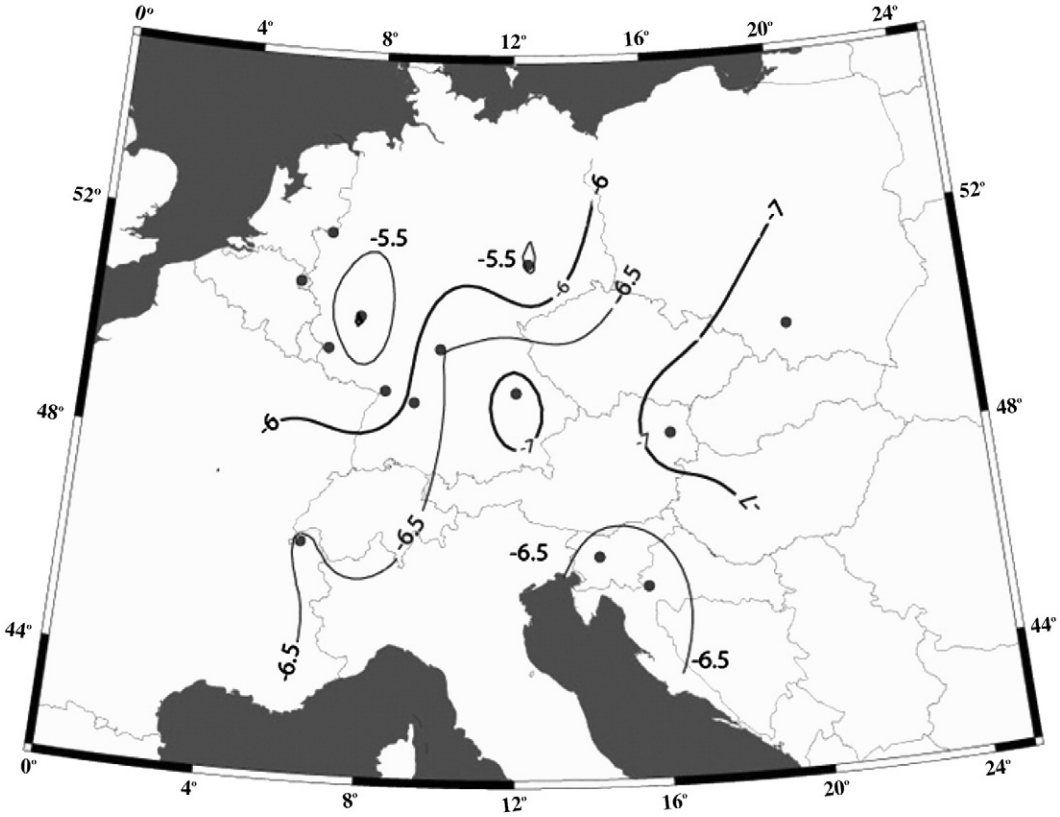
between the International Atomic Energy Agency (IAEA) and the World Meteorological Organization (WMO) to measure the content of oxygen and hydrogen isotopes in precipitation. The number of observation sites has been increasing since GNIP's inception in 1961, so it is essential to control for the variation of GNIP station records in time and space. The GNIP data set was sampled with the following criteria: (1) sites within the study area of 2.0°–28.0°E and 45.5°–52.0°N, (2) sites lower than 400 masl, (3) climate stations with at least a 20-yr record, and (4) climate stations with data for 90% of the possible sampling dates. To plot and understand seasonal trends in the isotopic composition of rainfall, warm-season (JJA), cold-season (DJF), and annual GNIP data were sampled (Figs. 4–6). Eighteen climate stations meet the annual sampling criteria, while the criteria allow only 14 sites for the analysis of JJA and DJF precipitation. The difference in sample sites creates local curves in the interpolated contours but does not affect the general trends in $\delta^{18}O$ contours. All results from the GNIP data set are expressed as weighted averages, where the sum of the product of $\delta^{18}O$ and precipitation amount is divided by the sum of the monthly precipitation amount. Weighted averages ensure that data from each sample site for each month have an effect proportional to the amount of precipitation. Land-snail shell carbonate is measured on the VPDB scale by common usage, and the GNIP data are measured against VSMOW. Therefore, the numerical values between the two data sets are not directly compared, and instead, the spatial distribution of shell $\delta^{18}O$ is compared with the observed isotopes in precipitation.

The modern measured $\delta^{18}O$ in precipitation decreases inland from the North Sea along a NNW–SSE gradient (Fig. 6). The countries bordering the North Sea consistently record the most enriched precipitation $\delta^{18}O$. The summer months in Belgium, the Netherlands, and northern Germany record isotope values of −5.5‰ VSMOW, with annual weighted averages of −7‰ VSMOW. Krakow and Vienna record the most depleted values with JJA values of −7‰ VSMOW and yearly values of −9‰ VSMOW. The yearly GNIP data depict a marginally greater range of values than JJA $\delta^{18}O$, with a 2‰ difference between Krakow and Beek. The gradient between Leipzig and Krakow



COUNTRY	TOWN	LATITUDE (N)	LONGITUDE (E)	ALTITUDE (m asl)	$\delta^{18}O$
Austria	Vienna	48.2500	16.3700	203	-7.25
Belgium	Beek	50.9200	5.7800	111	-5.94
Croatia	Zagreb	45.4899	15.5900	165	-6.11
France	Thonon –les -Baines	46.2200	6.2799	385	-6.54
Germany	Emmerich	51.8300	6.6000	43	-5.89
Germany	Karlsruhe	49.0200	8.3800	120	-5.76
Germany	Koblenz	50.3499	7.5800	97	-4.85
Germany	Leipzig	51.3499	12.4300	125	-5.37
Germany	Regensburg	49.0200	12.0700	377	-7.31
Germany	Stuttgart	48.8300	9.2000	315	-6.08
Germany	Trier	49.7500	6.6999	273	-5.77
Germany	Würtzburg	49.8000	9.8999	259	-6.47
Poland	Krakow	50.0700	19.8800	205	-7.27
Slovenia	Ljubljana	46.0400	14.3100	299	-6.36

Figure 4. GNIP data for June, July, and August. Data are a 20-yr weighted average (VSMOW). Sample sites are listed in alphabetical order by country, town. Contours depict 0.5‰ intervals.

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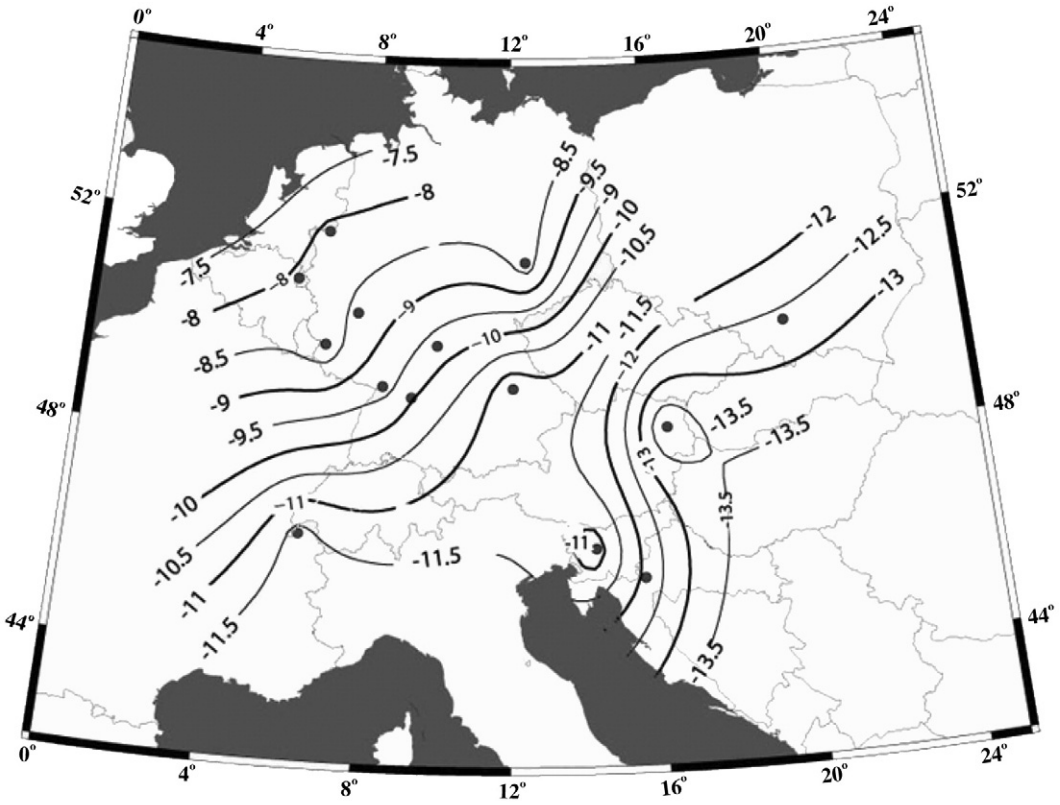

COUNTRY	TOWN	LATITUDE (N)	LONGITUDE (E)	ALTITUDE (m asl)	$\delta^{18}O$
Austria	Vienna	48.2500	16.3699	203	-14.00
Belgium	Beek	50.9200	5.7799	111	-7.88
Croatia	Zagreb	45.4899	15.59	165	-12.10
France	Thonon-Les_Bains	46.2199	6.2799	385	-11.67
Germany	Emmerich	51.8299	6.5999	43	-8.14
Germany	Karlsruhe	49.0200	8.3800	120	-9.30
Germany	Koblenz	50.3500	7.5799	97	-6.70
Germany	Leipzig	51.3500	12.4300	125	-8.20
Germany	Regensburg	49.0200	12.0700	377	-11.40
Germany	Stuttgart	48.8299	9.2000	315	-9.96
Germany	Trier	49.7500	6.7000	273	-8.15
Germany	Würzburg	49.7999	9.9000	259	-9.74
Poland	Krakow	50.0699	19.8800	205	-12.61
Slovenia	Ljubljana	46.0400	14.3100	299	-10.70

Figure 5. GNIP data for December, January, and February. Data are a 20-yr weighted average (VSMOW). Sample sites are listed in alphabetical order by country, town. Contours depict 0.5‰ intervals.

increases for DJF and yearly values compared to the summer. The difference between the values at Leipzig and Krakow is 1‰ for JJA, 2‰ for an annual average, and 4‰ for DJF. Ljubljana and Zagreb are consistently enriched in $\delta^{18}O$ compared to the values of surrounding locations, suggesting a Mediterranean source of water vapor. Although many fossil sample sites in this study are from Hungary, no Hungarian GNIP sites are included simply because Hungarian stations have only been reporting tritium and not oxygen isotopes in precipitation for the last 20 yr.

The oxygen isotope values for the modern genera were gridded using the Generic Mapping Tool's (GMT) geostatistical interpolator. Each sample site does not include each snail genus, and each site contains a varying amount of data. Isotope values were interpolated for the range of 4°–20°E and 45°–52°N to encompass every sample site but not to extrapolate beyond their locations. The modern land-snail shells portray a N–S gradient, with $\delta^{18}O$ values decreasing inland toward the Alps (Fig. 2). The range of modern oxygen isotopes in land-snail shell carbonate is 2‰, which is consistent with modern observed values for the yearly average $\delta^{18}O$ values over the same geographic area (Rozanski et al., 1993).

The similarity between the spatial distributions of oxygen isotopes in modern land snails (Fig. 2) with modern observational data (Figs. 4 and 6) supports the hypothesis that the $\delta^{18}O$ shell carbonate is a function of the isotopic composition of rainfall. The contours of oxygen isotopes in modern snail-shell carbonate are similar to the patterns of yearly mean $\delta^{18}O$ observed in precipitation. This correspondence in spatial pattern between the GNIP data and the modern shell data suggests that the direct effect of temperature on carbonate $\delta^{18}O$ is of relatively minor importance in the observed distribution of $\delta^{18}O$ in modern shells.

Comparison between spatial distribution of $\delta^{18}O$ in LGM and modern land-snail shells

Modern European land-snail shell $\delta^{18}O$ decreases inland from the North Sea and toward the Alps (Fig. 2) as does the $\delta^{18}O$ of modern

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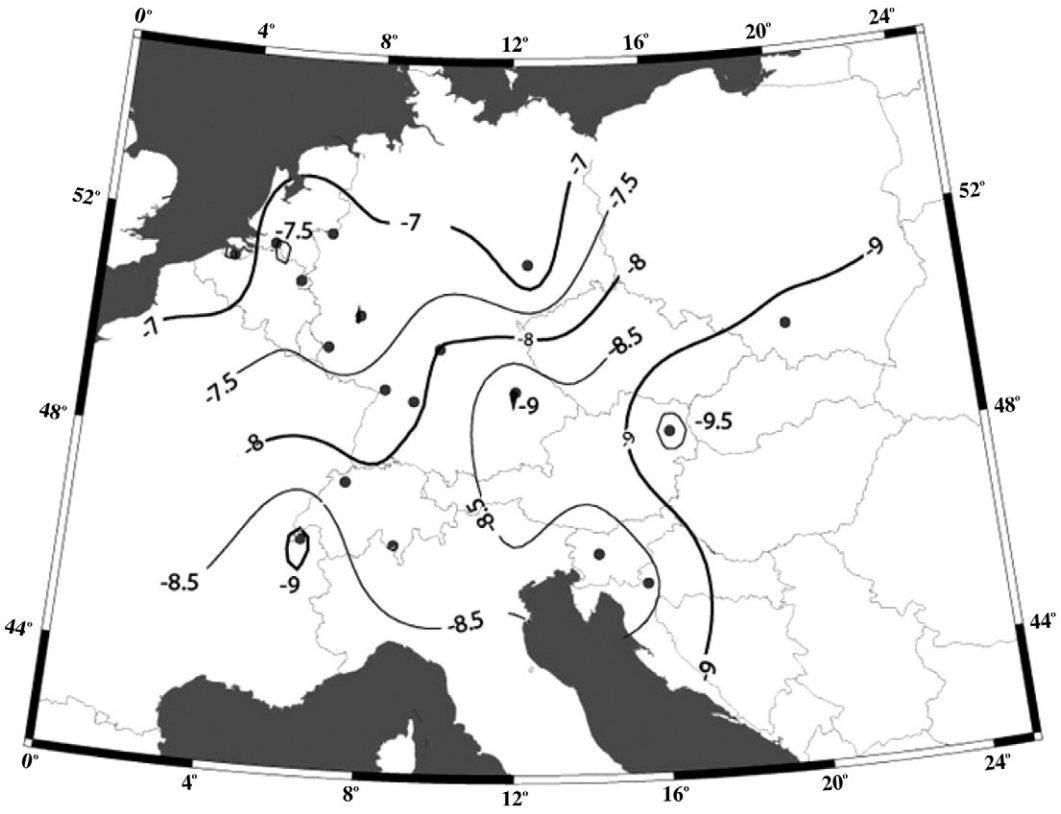

COUNTRY	TOWN	LATITUDE (N)	LONGITUDE (E)	ALTITUDE(m asl)	$\delta^{18}O$
Austria	Vienna	48.2500	16.3699	203	-9.69
Belgium	Beek	50.9200	5.7799	111	-7.08
Belgium	Braakman	51.3000	3.7500	2	-6.46
Croatia	Zagreb	45.4899	15.59	165	-8.33
France	Thonon-Les_Bains	46.2199	6.2799	385	-9.13
Germany	Emmerich	51.8299	6.5999	43	-7.19
Germany	Karlsruhe	49.0200	8.3800	120	-7.81
Germany	Koblenz	50.3500	7.5799	97	-6.94
Germany	Leipzig	51.3500	12.4300	125	-6.51
Germany	Regensburg	49.0200	12.0700	377	-9.06
Germany	Stuttgart	48.8299	9.2000	315	-7.90
Germany	Trier	49.7500	6.7000	273	-7.32
Germany	Würzburg	49.7999	9.9000	259	-8.05
Netherlands	Gilze-Rijen	51.5700	4.9300	11	-7.57
Poland	Krakow	50.0699	19.8800	205	-9.17
Slovenia	Ljubljana	46.0400	14.3100	299	-8.15
Switzerland	Locarno	46.1700	8.7799	379	-8.01
Switzerland	Weil am Rhein	47.3000	7.400	249	-8.10

Figure 6. GNIP data for annual weighted average $\delta^{18}O$ (VSMOW) composition of precipitation. Contours depict 0.5‰ intervals. Data are from a 90% complete record over 20 yr.

precipitation (Fig. 6). The deflection in $\delta^{18}O$ values near Switzerland and northern Italy demonstrates the altitudinal effect of topography on oxygen isotope in precipitation, and as only sites lower than 400 masl were samples, no data are present from the Alps. No modern shells were sampled in Hungary or Serbia, so it is unknown if the oxygen isotopic composition of modern land-snail shells would also record the influence of the Mediterranean precipitation source. The oxygen isotopic composition of modern gastropod shells reflects a north or northwest source of precipitation (Fig. 2). Modern contours of the oxygen isotope composition of land-snail shells are almost perpendicular to the spatial distribution of $\delta^{18}O$ in LGM snails (Figs. 1 and 2). LGM shell $\delta^{18}O$ depicts a gradient with $\delta^{18}O$ declining toward the ENE, implying a midlatitude Atlantic source (Fig. 1). Balkan LGM samples show the influence of a Mediterranean source, with $\delta^{18}O$ values decreasing northward. This difference in gradient direction agrees with the concept of a southward displacement of the North Atlantic Drift during the LGM due to increased sea-ice extent (Smith et al., 2003) and therefore lack of evaporation from the Norwegian and North Seas even in summer then.

The absolute values of $\delta^{18}O$ in both modern and fossil snail shells are remarkably similar, and in fact, the modern shell averages are more negative. The LGM snails can only possibly be active during summer months when temperatures are greater than 6 °C (Lécolle, 1985). Both the seasonality of $\delta^{18}O$ in precipitation and the fact that land snails hibernate if mean monthly temperatures are lower than 6 °C (Lécolle, 1985) suggest that LGM snails are enriched in ^{18}O versus sampling yearly precipitation. The seasonality of European LGM precipitation suggests that LGM snails are sampling only summer precipitation and are enriched in ^{18}O relative to what they would be if they were sampling yearly precipitation.

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Although temperature may have some effect on the shell $\delta^{18}O$, if all of the LGM spatial isotopic change were due to temperature, there would be a 16 °C increase toward the interior of Europe, which is about 4 or 5 times the present difference. Therefore, the isotopic gradient in precipitation must be the primary factor in controlling pulmonate gastropod $\delta^{18}O$ in order for the contrast between the modern and LGM spatial distribution of $\delta^{18}O$ in gastropod carbonate to emerge (Figs. 1 and 2). The spatial distribution of $\delta^{18}O$ in modern land-snail shells portrays a dramatic shift in the orientation and direction of isotope contours between the LGM and the present day.

Conclusion

The spatial pattern of $\delta^{18}O$ in modern shells generally corresponds with the distribution of observed oxygen isotopes in rainfall, suggesting that changes in shell $\delta^{18}O$ content reflects variation in precipitation $\delta^{18}O$. Temperature and precipitation amount do not appear to affect land-snail shell $\delta^{18}O$ in humid regions significantly, but the seasonality of snail activity plays a large role in the gastropod shell $\delta^{18}O$. This supports conclusions from recent studies (Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005) and must be taken into account when creating time-slice maps of oxygen isotope variability in land-snail carbonate. Due to the environmental conditions in which land snails are alive and active, LGM snails can only sample warm-season precipitation. The difference between modern and LGM ocean water is only 1‰ VSMOW (Shrag et al., 2002), making the similarity in the range of modern and fossil $\delta^{18}O$ values entirely plausible.

The spatial distribution of $\delta^{18}O$ values in modern and fossil gastropods from Central European loess is used to identify the principal water-vapor trajectories during the last glacial maximum and today. Modern land-snail $\delta^{18}O$ values suggest a North Sea and North Atlantic source, with water vapor moving southeastward toward the Alps. LGM gastropod $\delta^{18}O$ values imply a more southerly tropical to mid-Atlantic source, with $\delta^{18}O$ declining to the ENE. Predictions of LGM sea-ice extent as far south as 50°N during the LGM (Renssen and Vandenberghe, 2003; Smith et al., 2003) suggest minimal evaporation from the northern North Atlantic. The increase in sea-ice cover implies that LGM water vapor could not originate from the northern North Atlantic. Instead, storm tracks were shifted southward from their present location for both summer and winter months (Smith et al., 2003). The spatial distribution of $\delta^{18}O$ in fossil land-snail shell carbonate supports the suggestion of more southerly summer storm tracks and extensive sea-ice during the LGM (Smith et al., 2003). The LGM carbonate oxygen isotope decrease to the ENE, as opposed to the modern decrease along a NNW–SSE gradient, signifying a change in the storm tracks from the modern trajectory of air masses across Central Europe.

It is anticipated that the isotopic composition of land-snail shells will provide a valuable tool in testing atmospheric general circulation models (AGCM). The $\delta^{18}O$ information from shell carbonate can be used as a supplemental tool when investigating time-slice maps of the distribution of oxygen isotopes in precipitation. Fossil gastropods can be collected from a specific period. These attributes allow land-snail shells to be used as an independent data set that can constrain atmospheric general circulation model simulations extending back into the Late Pleistocene.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yqres.2010.03.001.

References

Araguas-Araguas, L., Froehlich, K., Rozanski, K., 2000. Deuterium and oxygen-18 isotope composition of precipitation and atmospheric moisture. Hydrological Processes 14, 1341–1355.
Balakrishnan, M., Yapp, C.J., 2004. Flux balance models for the oxygen and carbon isotope composition of land snail shells. Geochimica et Cosmoschimica Acta 68, 2007–2024.
Balakrishnan, M., Yapp, C.J., Theler, J.L., Carter, B.J., Wycoff, D.G., 2005. Environmental significance of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ values of modern land-snail shells from the southern great plains of North America. Quaternary Research 63, 15–30.
Boenick, W., Frechen, M., 2001. The loess record in sections at Koblenz-Metternich and Tonchesberg in the Middle Rhine Area. Quaternary International 76/77, 201–209.
Buch, M.W., Zöller, L., 1990. Gliederung und Thermolumineszenz-Chronologie der Würmloesse in Raum Regensburg, Eiszeitalter und Gegenwart, 40, 63–84.
Colonese, A.C., Zanchetta, G., Fallick, A.E., Martini, F., Manganelli, G., Lo Vetro, D., 2007. Stable isotope composition of Late Glacial land snail shells from Grotta del Romito (Southern Italy): paleoclimatic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 254, 550–560.
Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochimica et Cosmogenica Acta 12, 133–149.
Craig, H., 1961. Standard for reporting concentvaluesns of deuterium and oxygen-18 in natural waters. Science 133 (3467), 1833–1834.
Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.
Dawson, A.G., 1992. Ice Age earth; late Quaternary geology and climate. Routledge, London. In: Denton, G.H., Hughes, T.J. (Eds.), The Last Great Ice Sheets. Wiley-Interscience, New York.
Frechen, M., 1999. Upper Pleistocene loess stratigraphy in southern Germany. Quaternary Geochronology 18, 243–269.
Frechen, M., Zander, A., Cílek, V., Ložek, V., 1999. Loess chronology of the Last Interglacial/Glacial cycle in Bohemia and Moravia, Czech Republic. Quaternary Science Reviews 18, 1467–1493.
Frechen, M., van Vleit-Lanoë, B., Van den Haute, P., 2001. The upper Pleistocene loess record at Harmignies/Belgium—high resolution terrestrial archive of climate forcing. Palaeogeography, Palaeoclimatology, Palaeoecology 173, 175–195.
Frenzel, B., Pesci, B., Velichko, A.A. (Eds.), 1992. Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere. INQUA/Hungarian Academy of Sciences, Budapest.
Ganopolsksi, A., Rahmstorf, S., 2001. Rapid changes of glacial climate simulated in a coupled climate model. Nature 409, 153–158.
Goodfriend, G.A., 1991. Holocene trends in ^{18}O in land snail shells from the Negev desert and their implications for changes in rainfall source areas. Quaternary Research 11, 417–426.
Goodfriend, G.A., 1992. The use of land snail shells in paleoenvironmental reconstruction. Quaternary Research 35, 417–426.
Goodfriend, G.A., Ellis, G.L., 2002. Stable carbon and oxygen isotopic variations in modern Rabdotus land snail shells in the southern Great Plains, USA, and their relation to environment. Geochimica et Cosmochimica Acta 66, 1987–2002.
Goodfriend, G.A., Magaritz, M., Gat, J.R., 1989. Stable isotope composition of land shail body water and its relation to environmental waters and shell carbonate. Geochimica et Cosmochimica Acta 53, 3215–3221.
Grossman, E.L., Ku, T.L., 1986. Oxygen and carbon isotope fractionation in biogenic aragonite-temperature effects. Chemical Geology 59, 59–74.
Guiot, J., deBeaulieu, J.-L., Cheffafi, R., David, F., Ponel, P., Reille, M., 1993. The climate in Western Europe during the last glacial/interglacial cycle derived from pollen and insect remains. Palaeogeography, Palaeoclimatology, Palaeoecology 103, 73–94.
Guiot, J., Torre, F., Jolly, D., Peyron, O., Boreux, J., Cheddadi, R., 2000. Inverse vegetation modeling: a tool to reconstruct palaeoclimates under changed CO_2 conditions. Ecological Modelling 127, 119–140.
Hatté, C., Fontugne, M., Rousseau, D.D., Antoine, P., Zöller, L., Tisnérat-Laborde, N., Bentaleb, I., 1988. $\delta^{13}C$ variations of loess organic matter as a record of the vegetation response to climatic changes during the Weichselian. Geology 26, 583–586.
Kageyama, M., Laîne, A., Abe-Ouchi, A., Braconnot, P., Cortijio, E., Crucifix, M., de Vernal, A., Guiot, J., Hewett, A., Kitoh, A., Kucera, M., Marti, O., Ohgaito, R., Otto-Bliesner, B., Peltier, W.R., Rosell-Melé, A., Vettoretti, G., Weber, S.L., Yu, Y., MARGO Project Members, 2006. Last Glacial Maximum temperatures over the North Atlantic, Europe and western Siberia: a comparison between PMIP models, MARGO sea-surface temperatures and pollen-based reconstructions. Quaternary Science Reviews 25, 2082–2102.
Kerney, M.P., Cameron, R.A.D., Riley, G., 1987. A Field Guide to the Land Snails of Britain and Northwest Europe. William Collins Sons and Co., London.
Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayea, A., Weinelt, M., Chen, M.-T., Mix, A.C., Barrows, T.T., Cortijo, E., Duprat, J., Juggins, S., Waelcroeck, C., 2005. Reconstruction of sea-surface temperatures from assemblages of planktonic foraminifera: multi-technique approach based on geographically constrained calibvaluesn data sets and its application to glacial Atlantic and Pacific oceans. Quaternary Science Reviews 24, 951–998.
Lécolle, P., 1985. The oxygen isotope composition of land snail shells as a climatic indicator: applications to hydrogeology and paleoclimatology. Chemical Geology 58, 157–181.
Lécolle, P., Létolle, R., 1990. Paléotempératures déduites de la composition isotopique des tests de Gastéropodes terrestres and des travertins de al vallée de la Seine. In: Lécolle, F. (Ed.), Les Tufs et Travertins Quaternaires des Bassins de la Seine et de la Somme, et des Regions Limitrophes, Centre de Géomorphologie, Caen, France, Bull. no. 38, pp. 79–92.
Leone, G., Bonadonna, F., Zanchetta, G.I., 2000. Stable isotope record in mollusca and pedogenic carbonate from Late Pliocene soils of Central Italy. Palaeogeography Palaeoclimatology Palaeoecology 163, 115–131.

Lösceher, M., Zöller, L., 2001. Lössforschung im nordwestlichen Kraichgau. Jahresberichte und Mitteilungen des Oberrheinischen Geologishen Vereines 83, 317–326.
Ložek, V., 1972. Holocene interglacial in Central Europe and its land snails. Quaternary Research 2 (3), 327–334.
Magaritz, M., Heller, J., Volokita, M., 1981. Land–air boundary environment as recorded by the $^{18}O/^{16}O$ and $^{13}C/^{12}C$ isotope values in the shells of land snails. Earth and Planetary Science Letters 52, 101–106.
Mix, A., Bard, E., Schneider, R., 2001. Environmental Processes of the Ice Age: Land, Oceans, Glaciers (EPILOG). Quaternary Science Reviews 20, 627–657.
Oches, E.A., McCoy, W.D., 1995a. Amino acid geochronology applied to the correlation and dating of Central European loess deposits. Quaternary Science Reviews 14, 767–782.
Oches, E.A., McCoy, W.D., 1995b. Aminostratigraphic evaluation of conflicting age estimates for the "Young Loess" of Hungary. Quaternary Research 44, 160–170.
Oches, E.A., McCoy, W.D., Gneisser, D., 2000. Aminostratigraphic correlation of loess–paleosol sequences across Europe. In: Goodfriend, G.A., Collins, K.J., Fogel, M.L., Macko, S.A., Wehmiller, J.F. (Eds.), Perspectives in Amino Acid and Protein Geochemistry. Oxford University Press, NY.
Pésci, M., 1979. Lithostratigraphical subdivision of the loess profiles at Paks. Act Geologica Academiae Scientiarium Hungaricae 22, 409–418.
Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J.-L., Bottema, S., Andrieu, V., 1998. Climatic reconstruction in Europe for 18,000 yr B.P. from pollen data. Quaternary Research 49, 183–196.
Peyron, O., Bégeot, C., Brewer, S., Heiri, O., Magny, M., Millet, L., Ruffaldi, P., Van Campo, E., Yu, G., 2005. Lateglacial climate in the Jura Mountains (France) based on different quantitative reconstruction approaches from pollen, lake-levels and chironomids. Quaternary Research 64, 197–211.
Pye, K., 1995. The nature, origin and accumulation of loess. Quaternary Science Reviews 14, 653–667.
Renssen, H., Vandenberghe, J., 2003. Investigation of the relationship between permafrost distribution in NW Europe and extensive winter sea-ice cover in the North Atlantic Ocean during the cold phases of the Last Glaciation. Quaternary Science Reviews 22, 209–223.
Rousseau, D.D., Antoine, P., Hatté, C., Lang, A., Zöller, L., Fontugne, M., Ben Othman, D., Luck, J.M., Moine, O., Labonne, M., Bentaleb, I., Jolly, D., 2002. Abrubt millennial climatic changes from Nussloch (Germany) Upper Weichselian eolian records during the Last Glaciation. Quaternary Science Reviews 21, 1577–1582.
Rozanski, K., Araguas-Araguas, L., Gonfiantini, R., 1993. Isoptic pattern in modern global precipitation. In: Swart, P.K., Lohman, K.C., McKenzie, J., Savin, S. (Eds.), Climate Change in Continental Isotopic Records. : Geophysical Monograph, vol. 78. American Geophysical Union, Washington, pp. 1–36.
Shrag, D.P., Adkins, J.F., McIntyre, K., Alexander, J.L., Hodell, D.A., Charles, C.D., McManus, J.F., 2002. The oxygen isotopic composition of seawater during the last glacial maximum. Quaternary Science Reviews 21, 331–342.
Smith, L.M., Miller, G.H., Otto-Bliesner, B., Shin, S., 2003. Sensitivity of the Northern Hemisphere climate system to extreme changes in Holocene Arctic sea ice. Quaternary Science Reviews 22, 645–658.
Stevens, T. (2003) Aminostratigraphy of mid to late Pleistocene loess in middle Europe, M.S. Thesis, University of Massachusetts, Amherst.
Thompson, R., Cheny, S., 1996. Raising Snails. National Agriculture Library Special Reference Briefs. NAL SRB 96-05.
Ward, D., Slowtow, R., 1992. The effects of water availability on the life history of the desert snail *Trochoidea seetzeni*: an experimental field manipulation. Oecologia 90, 572–580.
Yanes, Y., Romanek, C.S., Delgado, A., Brant, H.A., Noakes, J.E., Alonso, M.R., Ibanez, M., 2009. Oxygen and carbon stable isotopes of modern land snail shells as environmental indicators from a low-latitude oceanic island. Geochimica et Cosmochimica Acta 73, 4077–4099.
Yapp, C.J., 1979. Oxygen and carbon isotope measurements of land-snail shell carbonate. Geochimica et Cosmochimica Acta 43, 629–635.
Yates, T.J.S., Spiro, B.F., Vita-Finzi, C., 2002. Stable isotope variability and the selection of terrestrial mollusc shell samples for C-14 dating. Quaternary International 87, 87–100.
Zanchetta, G., Leone, G., Fallick, A.E., Bonadonna, F.P., 2005. Oxygen isotope composition of living land snail shells: data from Italy. Palaeogeography, Palaeoclimatology, Palaeoecology 223, 20–33.
Zöller, L., Wagner, G., 1990. Thermoluminescence dating of loess – recent developments. Quaternary International 7/8, 119–128.
Zöller, L., Stremme, H., Wagner, G., 1988. Thermolumineszenz-Datierung and Löss-Paläoboden-Sequenzen von Nieder-. Mittel-. Und Oberrhein/Bundesrepublik Deutschland. Chemical Geology (Isotope Geoscience Section) 73, 39–62.

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