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Paleoclimatic Reconstruction Using Mutual Climatic Range on Terrestrial Mollusks

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Terrestrial mollusks, easily identified in Quaternary sediments, represent a reliable tool for quantitative estimates of environmental parameters. Our study, comparing the species distribution with meteorological parameters in Europe, shows that mean temperature of the coldest month and annual thermal magnitude are the most important forcing parameters. This survey allows us to adapt the mutual climatic range (MCR) method to terrestrial mollusk assemblages following two main steps. A set of assemblages from different European regions (northern Norway to southern France) is used to apply the method to present-day mollusks. The reconstructed values describe the latitudinal temperature gradient prevailing over Europe. However, the comparison between the reconstructed and the measured values indicates a shift, similar to that observed, with the same method applied to beetle assemblages. Thus, estimates must be calculated after the reconstruction is tuned with the observations. The results from the modern mollusk assemblages indicate that the MCR method can be safely applied to reconstructing temperatures from terrestrial mollusk assemblages in any worldwide Quaternary sequence. A trial application is made on Late Pleistocene assemblages from Achenheim (Alsace, France).

Key Words: **terrestrial mollusks; mutual climatic range; Europe; Quaternary; continental paleoclimatology; quantitative temperature estimates.**

INTRODUCTION

Temperature and moisture are the main factors that constrain the physiology and life cycle of terrestrial mollusks. Each species has a thermal interval controlling its activity (Pelseneer, 1935; Dainton, 1954; Franc, 1968b; Sacchi and Testard, 1971; Chevallier, 1982; Watabe, 1983; Rollo, 1991), its growth (Pelseneer, 1935; Uminski, 1975; Chevallier, 1982), its reproduction (Pelseneer, 1935; Bouillon, 1956; Franc, 1968b; Gomot *et al*., 1986; Gomot and Griffond, 1993), and its physiological functions (Pelseneer, 1935; Blazka, 1953; Langley, 1979; Armitage and Stinson, 1980; Biannic *et al*., 1995). Therefore these different thermal ranges determine specific wider thermal domains of life, and outside the ranges the species cannot survive. In comparison, moisture or precipitation cannot be determined so reliably. Indeed, experiments considering the influence of moisture variations on mollusks do not yield results as precise as those that fows on temperature (Pelseneer, 1935; Blazka, 1953; Chevallier, 1982; Phifer and Prior, 1985; Rollo, 1991; Biannic *et al*., 1995). Thus, as the link between moisture and precipitation is not obvious, any reconstruction of moisture and precipitation using mollusks evidence appears difficult at present.

Terrestrial mollusks are indices of both vegetation type and climate, permitting them to be grouped in ecological clusters

(Lozek, 1964; Puisségur, 1976). They are highly sensitive to environmental variation and provide reliable record of their biotope (Light and Killeen, 1996). The time response of malacofaunas to environmental changes, especially biome disappearance, is less than 50 years (Light and Killeen, 1996), indicating that modern distributions are in equilibrium with present environments. Mollusk shells are well preserved in Quaternary sediments, particularly in loess deposits, and can be identified at the species level using their form and ornamentation (Lozek, 1964; Puisségur, 1976), even though they are often broken (mainly large species). Consequently, biological qualitative information (i.e., species recognition) is generally preserved after the burial of the individuals. In addition, an important proportion of the quantitative information, lost by breakage, can be recovered by applying numerical corrections on identified and counted fragments (Puisségur, 1976). These observations led Lozek (1964) to consider the possibility that the ecological tolerances of each species are maintained through the Quaternary (Lozek, 1964). Therefore, since terrestrial mollusks record ecological and climatic variations, they can provide an excellent proxy from which to extract palaeoenvironmental information.

In parallel with new biological indicators used since the initial development of transfer functions on marine microfaunas (Imbrie and Kipp, 1971), several methods have been shown to estimate past climate and environmental parameters. The differences between these methods depend on the characteristics of the material and the modes of calculation (Guiot, 1994).

The relationship between terrestrial mollusks and climate is achieved by having a statistically valid number of samples from a present area that is large enough to be representative of as many different types of assemblages and climates as possible. Sometimes, however, a determined area does not include the complete range of assemblage categories identified in a fossil sequence, and thus nonanalogues appear. In biological data sets of this type, two modes of calculation can be used: extrapolation and interpolation.

Extrapolation uses methods allowing the reconstruction of parameter values outside a reference data set (Fritts *et al*., 1971; Webb and Bryson, 1972; Guiot, 1986). However, the data-set values define a domain inside which a relationship between a proxy and a climate parameter can be established. Thus, as the relationship is not always valid outside this domain, these methods are not recommended. Furthermore, in most cases, there are no means to confirm the calculated estimates (Guiot, 1994). Interpolation methods by comparison constrain the reconstructions only in the domain of the reference data-set values. These methods have been applied to different biological proxies: pollen (Overpeck *et al*., 1985; Guiot, 1987; Huntley and Prentice, 1988), lacustrine ostracods (Mourguiart *et al*., 1998), lacustrine diatoms (Gasse and Tekaia, 1983), rodents (Montuire, 1999), and mollusks (Rousseau, 1991). But even in these cases, problems of nonlinear response by the fauna or flora to a determined climatic parameter may occur inside the domain of the reference data set. This prevents reconstruction beyond intrinsic thresholds if no improvements are realized (Waelbroeck *et al*., 1998). The methods used vary according to the sensitivity of the organisms to the environment and the time interval investigated.

From terrestrial mollusks assemblages, temperature and precipitation reconstructions have previously been calculated using the analogues method (Rousseau, 1991; Rousseau *et al*., 1994; Rousseau *et al*., 1998a). However, the present analogue assemblages are located only in Western Europe, and the use of this method is strictly restricted to this area. Furthermore, the possibility of nonanalogous assemblages cannot be excluded. Such assemblages yield only approximate reconstructions. Otherwise, this method has already been successfully adapted and applied to different organisms such as insects (Atkinson *et al*., 1987; Elias, 2000), pollen (Peyron, 1998) and rodents, following a similar principle called the Hokr method (Chaline and Brochet, 1989). By taking into account these methodological restrictions, we decided to test the use of the mutual climatic range (MCR) method on mollusk assemblages, which it seems possible to apply throughout the range of terrestrial mollusks.

MATERIAL

Modern Data

The MCR method employs the modern geographic distributions of the different Pulmonate and Prosobranch species identified in the fossil assemblages used. For Europe, these were published in the malacological atlas of Kerney *et al.* (1983).

The corresponding European meteorological data set has been extracted from a global database (Leemans and Cramer, 1991). This includes 1735 stations providing minimal and maximal mean monthly temperatures for Europe between 72°N and 41°N and between 11°W and 33°E (Fig. 1). The values of these parameters, linked with the species geographic distributions, allows the definition of specific climatic ranges (SCR) (Atkinson *et al*., 1986). Furthermore, as malacological distributions are based on modern samples (Kerney *et al*., 1983) and climatic data on records obtained between 1941 and 1960 (Leemans and Cramer, 1991), we consider that the published malacological distributions are in accord with the climatic data used. Indeed, numerous cold-resistant species currently live in Scandinavia. Such a pattern implies that mollusk colonization during the Holocene of this formerly glaciated area was rapid. The northward extension of the geographic distributions of determined species, related to the present interglacial conditions, can then be assumed as completed in this area. However, if present climatic conditions related to global warming continue to extend northward, the geographical distributions, $T_{\min}$, and $T_{\max}$ estimates will be overestimated.

The MCR method was calibrated using modern mollusk samples taken from six regions distributed parallel to the present N–S European thermal gradient (Fig. 2). These regions are Karasjakk (Norway) (Andersen and Halvorsen, 1984), Abisko (Sweden) (Nilsson, 1968, 1987), Dovrefjell (Norway) (Pokryszko, 1989),

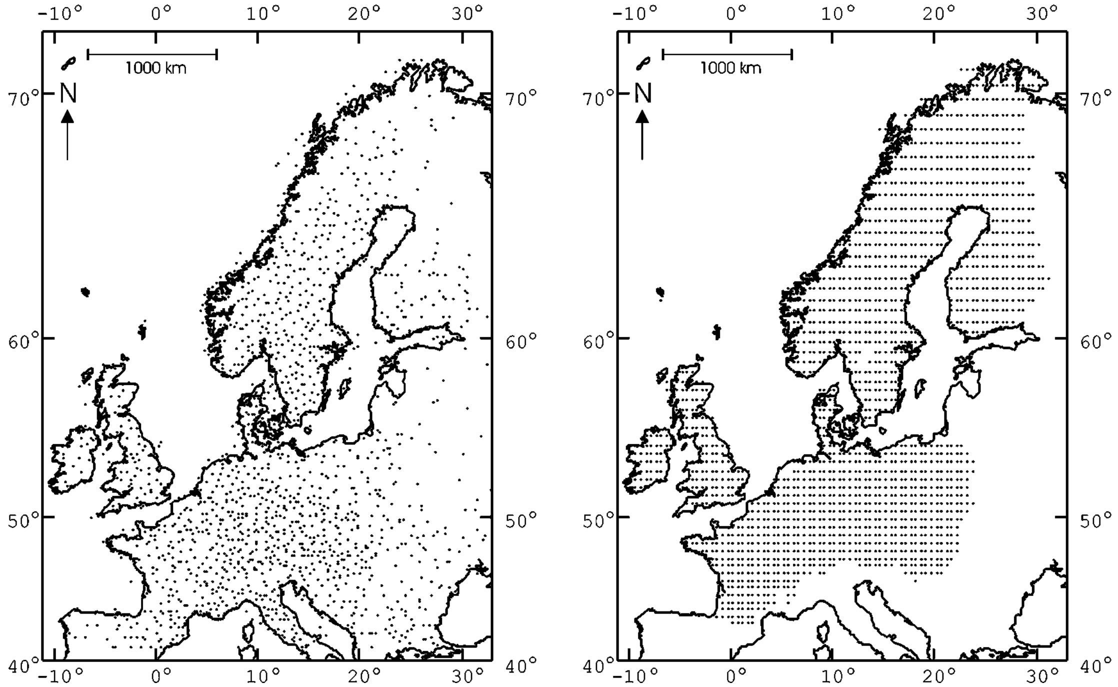

FIG. 1. Map showing the meteorological stations in Europe from the Leemans and Cramer (1991) database (on the left), and from the grid defined in this study (on the right).

Périgord (France) (Limondin, 1990), Burgundy (France) (Puisségur, 1976; Rousseau *et al.*, 1994), and Queyras (France) (Magnin, 1991; Rousseau *et al.*, 1994). In each region, samples were collected away from areas of noticeable modern human impact on the environment (Cameron, 1978; Kerney *et al.*, 1983; Limondin, 1990; Rousseau, 1993).

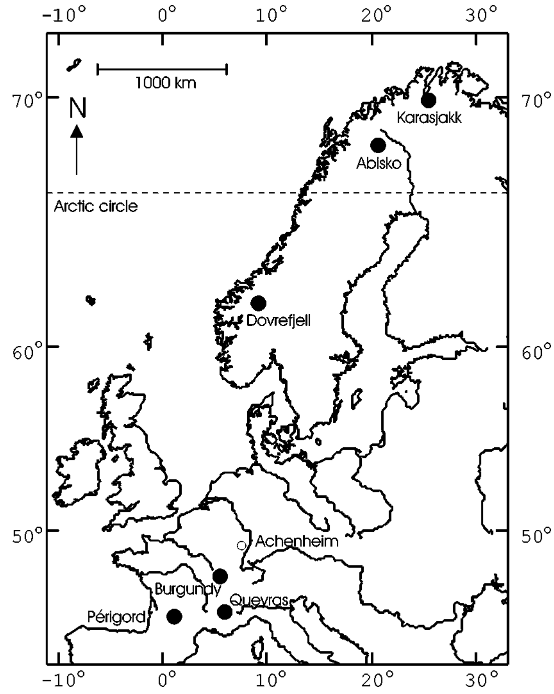

FIG. 2. Location of the present sampling regions (filled circles) and fossil site (empty circle). Filled circles include several sampling localities.

Fossil Data

Forty-four fossil assemblages were obtained from the Achenheim loess sequence, located 5 km west of Strasbourg (Alsace, France) (Fig. 2). This sequence contains a record of important climatic and environment changes for the last 500,000 yr. Furthermore, the last climatic cycle, and the related mollusk assemblages selected for this study, showed the strongest temperature variations (Rousseau and Puisségur, 1990). These assemblages, previously analyzed with the analogues method (Rousseau, 1991), are an appropriate set for allowing comparisons between both methods and for testing the reliability of the MCR method applied to terrestrial mollusks.

METHODS

Data Homogenization and Digitalization

The MCR method requires an adjustment of the original data. The meteorological stations yielding temperature values have a heterogeneous distribution over Europe. Consequently, after having defined a mesh of 0.5° in longitude and latitude, we used an artificial neural network (ANN) (Caudill and Butler, 1992) to estimate mean monthly temperatures at these knots (Fig. 1). We chose this method instead of any other weighted averaged interpolation because the thermal altitudinal gradient used by the latter was the same for all the mountains. This led to temperature underestimations, which reached 20°C in northern Scandinavia, although in the other regions their estimation is slightly more precise than those obtained from the artificial neural network.

The artificial neural network used in this study is composed of three layers of processors named neurodes. The input layer contains three neurodes (I-neurodes) for longitude, latitude, and elevation of the meteorological stations respectively. The output layer contains 12 neurodes (O-neurodes) corresponding to the monthly climatic parameters of the meteorological stations. The middle layer, linking the two others, is composed of several neurodes (M-neurodes), the number of which is adjusted after repeated attempts. Each M-neurode receives three sources of information, one per I-neurode, combining them and sending the result to each O-neurode. The O-neurodes combine the information they received from the M-neurodes and allow comparison of the final result with the observed climatic data. This method has already been described in detail by Peyron (1998). The estimated parameters are then homogeneously distributed in the studied zone.

The interpolated temperatures permitted the definition of isotherms which have been compared with those published by Wallen (1970). Results are similar, and local differences are lower than or equal to 2°C. Furthermore, the meteorological stations used in our database are more numerous than those used in Wallen's (1970) *World Survey of Climatology*. Thus, we assume that the results of our interpolations are reliable, and the very small differences observed are negligible.

To more easily link the observations to the climate data (Fig. 3), the geographic distribution of each species has been digitized using the same grid as is used for the meteorological stations. Presence and absence of species are respectively coded by one and zero at each knot.

Reconstructed Parameters

After the temperature and distribution data sets were determined, the next step of our study was to define the most appropriate temperature parameters for the reconstructions. Each digitized species distribution was compared with 12 digitized monthly temperature maps to determine the most significant ecological parameter on this mollusk distribution. In each case we computed the Akaike's (1973) criterion (AIC). This criterion is an extension of the maximum likelihood principle—that is, a decrease in the deviance induced by the addition of parameters is compensated for by an increase in this deviance proportional to the number of parameters added, as in

$$\mathrm{AIC} = -2 \sum_{i=1\mathrm{to}N} \ln(x_{\mathrm{i}} \mid \theta) + 2k,$$

where k is the degrees of freedom of the probabilistic model, and N is the number of sites used for the calculation (Akaike, 1973). Thus, this allows the rejection of parameters which do not induce a significant decrease of deviance. For different nonnested probabilistic models based on the same data set, the smallest AIC indicates the value that best fits the data set.

A precise generalized linear model will connect the species distribution (y) with a climatic parameter (x). As each species has a thermal optimum for life, we choose by default the quadratic polynomial to link the probability (p) of the expected species distribution (y) with a determined climatic parameter (x). The (y) response being binomial (absence $= 0$ and presence $= 1$), a logit link [logit $p = \ln(p/(1 - p))$] was used to avoid any important flattening of the function of probability, and therefore no constants are too small in its equation. Subsequently, the computation of AIC allows the evaluation of the correlation between a single monthly parameter and a species distribution.

Our computation, including geographic distribution and mean monthly temperatures, indicates that cold months are generally related to low AIC and warm months to high AIC. Such results demonstrate that cold temperatures are a more important limiting factor on the species distributions than warm ones. Furthermore, considering this criterion, there are not enough species in the malacological assemblages to allow a reliable reconstruction for each mean monthly temperature. Thus, as extreme mean monthly temperatures (February and August) cannot always be reconstructed, we preferred three parameters that refer to all the identified species: T_{min}, T_{max}, and T_{range}. T_{min} distribution includes the coldest mean monthly temperatures recorded at each knot of the grid, T_{max} the warmest, and T_{range} the annual thermal range, identical to the difference between T_{min} and T_{max}. The T_{min} data set is composed of values from January and February, and the T_{max} data set of values from July and August. The following calculation of the AIC was carried out on each probabilistic model, linking a geographic species distribution with one of the three parameters—T_{min}, T_{range}, and T_{max}—to validate which should be reconstructed.

Our calculations indicate that the limiting factors on the geographic distribution of the terrestrial mollusk species are, in ascending order of their AIC, T_{min}, T_{range}, and T_{max} for the majority of species. Moreover, for each species, comparison between the lowest AIC of mean monthly temperatures and T_{min} does not generally show a strong difference. This supports our reconstruction of T_{min} and T_{range}, which have the lowest AIC in the present study, and the deduction of T_{max} through their difference.

Mutual Climatic Range Method

The correspondence between digitized distributions of the species and climate allows the definition of SCR in a biplot diagram with T_{min} and T_{range}, respectively, on the *y* and *x* axes (Atkinson *et al.*, 1986) (Fig. 4). The superposition of the different SCRs for a determined assemblage defines the MCR which is the climatic space shared by all the species in the assemblage. As this MCR is sometimes restrained, its distribution on each axis is not necessarily normal or showing well-defined peaks. Thus, the median value of the MCR distribution was preferred to the mean and the mode and yielded the most probable estimate on each axis for a modern assemblage. Moreover, for the fossil assemblages, the most probable estimation requires

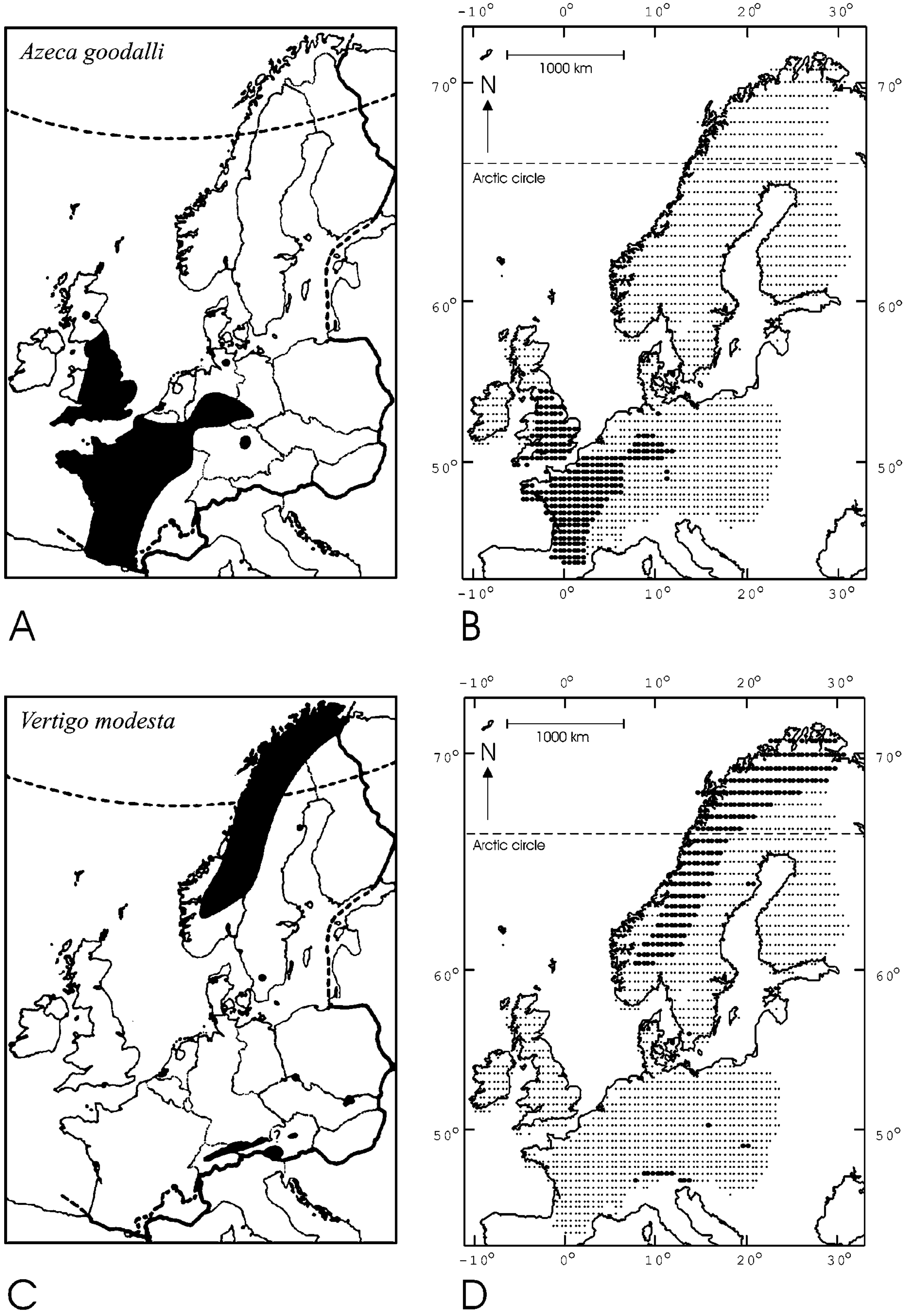

FIG. 3. Geographic distributions of the species *Azeca goodalli* and *Vertigo modesta* from the malacological atlas of Kerney *et al*. (1983) (A and C, respectively) and digitalized distributions with the grid defined in this study (B and D, respectively). On A and C, presence is represented by a black area; on B and D, it is characterized by large dots.

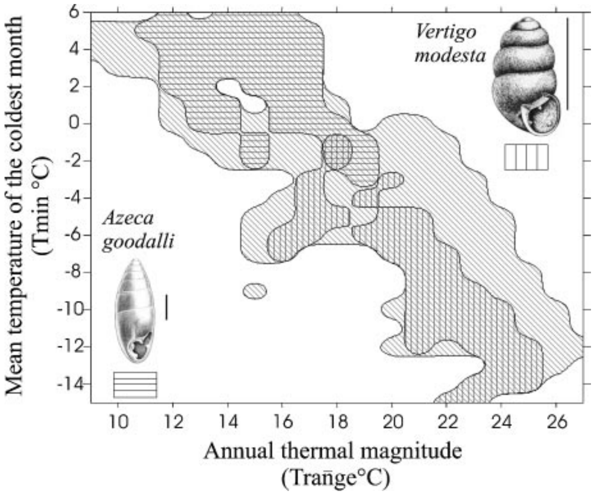

FIG. 4. Specific climatic ranges (SCR) and mutual climatic range (MCR) determined for the species *Azeca goodalli* (horizontal lines) and *Vertigo modesta* (vertical lines) and for the studied zone (diagonal lines). The SCRs are the climatic envelopes of the species, and the MCR is the climatic area shared by the envelopes of all the species of the assemblage. The length of the scale near shells is 3 mm.

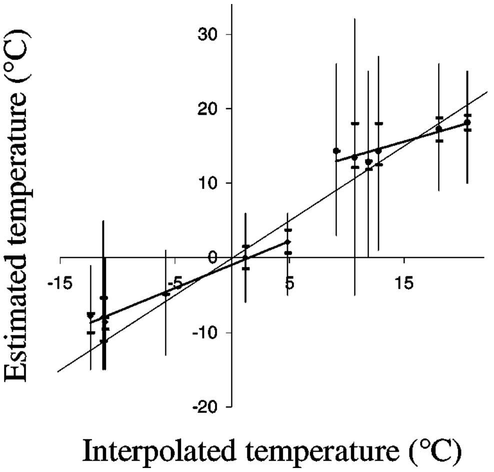

FIG. 5. Comparison between measured and estimated minimal ($T_{\min}$) and maximal ($T_{\max}$) monthly mean temperature temperatures of the six modern sampled regions. Each region gathers several sampled locations (Table 1). Each regional error margin (vertical lines) comprises the two extreme MCR limits from its local reconstructions. Each regional estimated mean temperature (black dots) is the mean of the values reconstructed from its samples. For each region, the two horizontal ticks limit the dispersion range of its local estimated mean temperatures.

an additional correction applied on the median value. For each reconstructed parameter, this correction is based on the equation of a linear regression between interpolated (from artificial neuronal network) and estimated (from MCR) values from a set of present assemblages from the studied area. Error margins of the parameter are the extreme values of the corresponding MCR (Atkinson *et al*., 1986).

RESULTS

Modern Samples

The method was first tested on modern assemblages. The interpolated values, at the geographic coordinates of these assemblages, are obtained from the modern data set using the artificial neural network defined previously. The reconstructed values were obtained from the mollusk assemblages using the MCR method. For the 65 assemblages of the six sampled regions, the interpolated $T_{\min}$s and $T_{\max}$s are included in the error margins of the reconstructed values.

In each of the six regions, the mean of the reconstructed values from the samples yielded the regional $T_{\min}$ and $T_{\max}$. The lowest and highest values of the error margins, for a determined area, represent the regional error margins (Table 1 and Fig. 5). The values of the regional $T_{\min}$ reconstructions of the three Scandinavian regions (Table 1) are not statistically different. In contrast, those of the three French areas are significantly different from each

TABLE 1
Interpolated and Estimated Temperatures for Modern European Assemblages

Region and (localities)	Mean $T_{\min}$ (°C)		Range of local estimations	Regional error margins	Mean $T_{\max}$ (°C)		Range of local estimations	Regional error margins
	Int.	Est.			Int.	Est.		
Karasjakk (4)	−11.1	−8.6	−9.6; −8	−15; 0	12.8	14.3	12.5; 18	1; 27
Abisko (10)	−12.4	−7.8	−10; −7.5	−15; −1	11.9	12.8	11.9; 13	0; 25
Dovrefjell (36)	−11.2	−7.9	−11.2; −5.4	−15; 5	10.7	13.5	12.1; 18	−5; 32
Queyras (1)	−5.8	−4.9	−4.9; −4.9	−13; 1	9.1	14.3	14.3; 14.3	3; 26
Bourgogne (7)	1.2	0.1	−1.4; 1.5	−6; 6	18.1	17.2	15.7; 18.8	9; 26
Périgord (7)	4.9	2.2	0.7; 3.7	−5; 6	20.6	18.2	17.1; 19.1	10; 25

Note. Int. are the modern interpolated values with the artificial neural network; and Est.- the modern estimated values with the mutual climatic range (MCR) method on mollusk assemblages. The estimated values of $T_{\min}$ have been calculated with the median applied on the MCR distributions along the $T_{\min}$ axis. The estimated values of $T_{\max}$ have been deduced from the difference between T_{range} and $T_{\min}$. The minimal value of the error margins is the minimal value for the MCR, and the maximal value is deduced by addition as $T_{\max}$. In the range of local estimations, the values are calculated for the entire locality of a region. For each region, the regional error margins are determined by taking the two extreme values of the MCRs boundaries for the entire localities.

other and from those in Scandinavia. The values of the regional T_{max} reconstruction of both the warmest French regions, Burgundy and Périgord, are significantly different from all the others. In both considered clusters, regional T_{max} is significantly equivalent.

These first results show that error margins are generally wider for T_{max} reconstructions (±13°C) than for T_{min} ones (±7°C). The proportionality of the range of the error margin with the value of the reconstructed T_{min} and T_{max} is an artifact. This is possibly due to the proportionality between the range of the error margin and the specific diversity of the assemblages. Indeed, the specific richness of an assemblage is positively correlated to the regional temperature (Kerney *et al.*, 1983). Consequently the MCR will be narrower.

The plot of the regional T_{min} and T_{max} values shows that the European thermal gradient is reconstructed, but that low values are overestimated whereas high values are underestimated. As a consequence, a linear regression has been calculated from the regional values for each parameter (Fig. 5). The equations used to correct the estimated values with regard to the observed ones are:

$$\text{for } T_{min}\text{: } [T_{calibrated}] = 0.63^{*}[T_{predicted}] + 9.00 \text{ with } r^2 = 0.99$$

$$\text{for } T_{max}\text{: } [T_{calibrated}] = 0.44^{*}[T_{predicted}] - 0.91 \text{ with } r^2 = 0.83.$$

The standard error of corrected values is lower than 1°C, thus ranging within the error margins. As the calibration also illustrates that a bias exists between modern estimated and measured temperature values, this correction is likewise used on fossil estimates to provide the best possible temperature reconstructions. As the values of the error margins depend mainly on the climate at the known limits of the geographic distributions of species, they are not subject to the same biases. Thus, these correction equations have not been applied to error margin values. The major problem identified with these error margins appears when, for all the species of an assemblage, there is only a single value in common as MCR. Indeed, extreme values are then identical to the estimated values without correction. Thus, the correction shifts the value outside the defined interval of the error margins. A solution is to use the extreme values of a broader MCR containing N-1 species for an N species assemblage (Fauquette *et al.*, 1998) and calculate a new most probable value on this MCR to keep coherency in the data.

Fossil Estimates

The 44 assemblages analyzed from the loess sequence at Achenheim have yielded reconstructions of T_{min} and T_{max} (Table 2). The maximal range for both parameters is around 5°C, between −4.9 and −0.1°C for T_{min} and between 10.5° and 15.5°C for T_{max}. The error margins of both parameters are significantly different. For T_{min} reconstruction, they extend from ±4 to ±10°C and for T_{max} from ±7 to ±18°C. Contrary to the modern assemblages analyzed previously, the range of the error margins is inversely proportional to the values of the reconstructed T_{min} and T_{max}. Then, if we assume that the relationship between the range of error margins and reconstructed parameters is an artifact due to the taxonomic diversity of the assemblages, this implies that at Achenheim climatic parameters other than

TABLE 2
Estimated Temperatures for Fossil Assemblages from Achenheim (Alsace, France)

			T_{min} corrected (°C)		T_{max} corrected (°C)	
Sample	Depth	Number of species	MCR range	Median MCR	Range	$T_{min} + T_{range}$
q26p	0.348	11	−9; 6	−1.9	6 to 29	14.6
q25p	0.522	5	−9; 6	−1.6	0 to 30	15.4
q24p	0.739	4	−7; 1	−4	8 to 23	13.8
q23p	1.001	5	−9; 6	−1.6	0 to 30	15.4
q22p	1.262	4	−9; 6	−1	0 to 29	15.8
q21p	1.653	3	−12; 6	−1.1	−3 to 30	15.8
q20p	2.088	2	−7; 1	−4	8 to 23	13.8
q19p	2.523	7	−7; 1	−3.7	9 to 23	13.6
s07p	2.784	6	−7; 1	−3.5	9 to 23	14.8
s08p	2.958	8	−7; 1	−3	9 to 23	15.2
q17p	3.306	9	−7; 1	−3.7	9 to 23	13.6
q16p	3.611	8	−7; 1	−3.7	9 to 23	13.6
q15p	4.046	7	−7; 1	−4	8 to 23	13.8
q14p	4.306	6	−7; 1	−3.7	9 to 23	13.6
q13p	4.481	6	−7; 1	−3.7	9 to 23	13.6
s10p	4.705	4	−9; 6	−1.6	0 to 30	15.4
s11p	5.046	5	−9; 5	−2.4	5 to 28	14.7
s12p	5.307	6	−7; 1	−3.5	9 to 23	14.8
s13p	5.655	5	−7; 1	−3.5	9 to 23	14.8
q11p	6.177	8	−7; 1	−3.7	9 to 23	13.6
s14p	6.525	4	−9; 5	−2.4	5 to 28	14.7
s15p	6.743	5	−9; 5	−2.4	5 to 28	14.7
s16p	7.134	5	−9; 5	−2.4	5 to 28	14.7
s17p	7.308	6	−9; 5	−2.4	5 to 28	14.7
s18p	7.482	6	−9; 5	−2.4	5 to 28	14.7
s19p	7.83	6	−9; 5	−2.4	5 to 28	14.7
s20p	8.352	6	−7; 1	−3.5	9 to 23	14.8
s21p	8.7	4	−9; 6	−1.6	0 to 30	15.4
s22p	9.178	5	−9; 6	−1.6	0 to 30	15.4
s23p	9.57	5	−9; 6	−1.6	0 to 30	15.4
s24p	10.005	4	−9; 6	−1.6	0 to 30	15.4
s26p	10.788	4	−9; 6	−1.6	0 to 30	15.4
s27p	11.223	4	−9; 6	−1.6	0 to 30	15.4
z24p	11.571	2	−14; 6	−1.8	−5 to 31	15.3
z23p	12.006	3	−12; 6	−1.4	−3 to 30	15.6
z22p	12.354	5	−12; 5	−2.6	−3 to 29	14.9
z21p	12.702	6	−9; 4	−2.5	6 to 28	14.9
z20p	13.18	3	−14; 5	−3	−5 to 30	14.5
z15p	15.008	4	−12; 5	−2.6	−3 to 29	14.9
z14p	15.356	6	−11; 5	−2.2	−2 to 29	15.2
z13p	15.704	4	−9; 6	−2.1	6 to 30	14.7
z12p	15.878	4	−9; 6	−2.1	6 to 30	14.7
z11p	16.269	2	−14; 6	−1.8	−5 to 31	15.3
q06p	16.704	5	−9; 6	−1.6	0 to 30	15.4

Note. Estimated values of T_{min} and T_{max} have been corrected with the respective equations of the linear regressions calculated for both clusters of modern assemblages. These corrective equations are not applied to margin values which are not calculated with the median as estimated values.

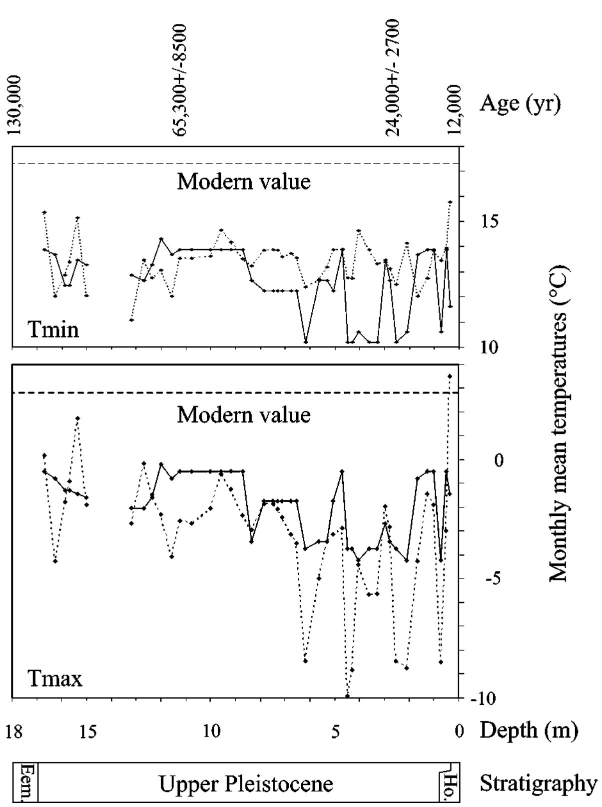

FIG. 6. Variations of $T_{\min}$ and $T_{\max}$ reconstructed from the malacological assemblages of Achenheim (Alsace, France) with the analogues method (dotted lines) and with the MCR method (straight lines). Ho. = Holocene; Eem. = Eemian. Temperatures reconstructed from the MCR and the analogue methods are represented by a straight line and a dotted line, respectively. For each assemblage, because error margins of estimates overlap, they were not plotted in order to clarify this scheme. TL dating are from Rousseau *et al.* (1998b), and the inferior boundaries of the Eemian and the Holocene are from Imbrie *et al.* (1984).

temperature were controlling the specific diversity. These may include moisture and/or precipitation.

The plot of the temperature estimates against depth yielded two curves with general trends corresponding to what may be expected for the last climatic cycle (Fig. 6). Barren samples during the Eemian and at the base of the Late Pleistocene prevented any temperature reconstructions. The $T_{\min}$ and $T_{\max}$ curves show similar trends but differences in detail.

Close to the base of the sequence, between 17 and 15 m depth, both curves show a slight decreasing trend from −1 to −2.5°C and from 14.5 to 13.5°C, punctuated by a cooling lower than 1°C for $T_{\max}$. Above the second barren zone, the estimates illustrate a strong two-step warming of around 2.5°C between 13 and 12 m depth. The temperature increases from −3 to −1°C and from 12.5 to 15°C. Subsequently, both curves indicate decreasing steps in temperature, between 12 and 6 m, from −1 to −2.5°C and 14.5 to 13°C, respectively. The two steps of the $T_{\min}$ curve are separated by a strong cooling reaching −4°C. This is followed by a strong and abrupt thermal oscillation between 6 and 1 m in both curves. The oscillations range between −5 and 0°C for $T_{\min}$ and 10.5 and 15.5°C for $T_{\max}$. The depth and magnitude of peaks in both curves correspond except at 3 m, where the magnitude of $T_{\max}$ is twofold that of $T_{\min}$. Furthermore, two important coolings occur around 6 and 2 m depth. In the last meter, both curves show a rising trend from −5 to −1°C and from 11 to 14.5°C, followed by a fall to 13°C for $T_{\max}$.

DISCUSSION

Intrinsic Problems of the MCR Method

The MCR method is based on a correspondence between species distribution and temperature. Each temperature reconstruction performed on present-day assemblages should have led to values equal to those measured from meteorological stations. Our study shows, as Atkinson *et al.* (1987) indicated with beetles, that a bias exists between interpolated and reconstructed values. A calibration on present-day data has been used to determine a correction to be applied to present-day and fossil temperature estimates. Does this mean that a correction, based on a local calibration, could be applied everywhere, or is a worldwide calibration required ?

A species distribution is frequently dependent on several environmental parameters. Indeed, if a species occurrence is constrained by a determined range of tolerance to a climate parameter, this range can shift under the influence of other parameters. If the calibration between the species presence and a climate parameter, established in a particular region is used to correct values of this parameter in another region, the correction will not be valid (Elias, 1997; Elias *et al.*, 1999). Only if the calibration could be carried out worldwide, or at least on the complete distribution, would the problem of shifting regional tolerance be solved. On the contrary, this worldwide calibration would smooth all the different regional climatic characteristics related to their geographic location (i.e., plain, mountain, or coast). Taking this problem, into account Elias *et al.* (1999) used regional calibrations, based on modern samples from areas with geographic characteristics similar to those of the considered fossil sites. Then the present reconstructed values from beetle assemblages best fit the observed parameters. However, such a method implies precise knowledge of the location of the fossil assemblages, and thus the determination of the boundaries of the present regional calibration area. Consequently, as the test of the MCR method on mollusk data has been realized to avoid the use of the analogues assemblages, this regional calibration has not been used in our study. This easier correction is then used by default and does not take into account what could be the origin of this bias. Indeed, it is observed in thermal reconstructions based on insects (Atkinson *et al.*, 1987) and mollusks (present study). For pollen (Fauquette *et al.*, 1998), this bias is not similarly noted, although this method was applied to Tertiary pollen; Farquette and colleagues used a pretreatment, gathering pollen species in ecological groups in the calculation of the most probable interval, so their MCR method is not similar to our technique. Consequently, their correlation coefficients cannot be compared with the bias we recognize in our study. Finally, the test of the Hokr method, applied to rodents (Chaline and Brochet, 1989) and using only one present-day fauna, does not provide a comparable data set to resolve this problem.

A first hypothesis is that this bias could be due to the incomplete species distributions used in the definition of the SCR, which is based only on the European malacological atlas of Kerney *et al.* (1983). Indeed, if the complete specific distributions are not available as plotted in Kerney's atlas (mainly in areas of extreme temperatures), the real extreme thermal limits of the SCR will not be reached. Thus, the reconstructions of $T_{\min}$ and $T_{\max}$ produced from the calculation of the most probable value will be respectively overestimated and underestimated. This hypothesis could explain the observed bias, but as it also has been detected in insects, for which the complete specific distributions were used, another explanation must be sought. Moreover, a lack of meteorological stations may not necessarily originate the bias, because this would imply that colder temperatures have not been recorded. Thus, as colder mean monthly temperatures mostly occur beyond the Petchora River (Russia), their occurrence in Finland is strongly improbable. Consequently, the low number of meteorological stations in Finland is not assumed to impose any bias. Finally, as the characteristics of the considered bias differ from those ($T_{\min}$ and $T_{\max}$ overestimated) proposed if northward species migration was at its origin, the latter hypothesis is rejected. Our assumption also considers restrained geographic distributions under any drastic environmental conditions before the geographic mapping of the species.

A second hypothesis is that the mode of calculation of the most probable value of the MCR, used for insects and mollusks, is not reliable. In both cases, the SCR are unweighted, and the number of individuals of the species is not taken into account. This calculation, as we used it, assumes that all the climatic couplets included in the MCR, and thus in each SCR, have the same weighting; this is probably incorrect. Moreover, the use of the number of individuals of each species could be used carefully. On the one hand, the relative abundance of the species can be due to taphonomic processes acting between the biocenose and the taphocenose. However, the shells, grouped in particular structures by water, are relatively well detected during the sampling. On the other hand, the relative abundance of the species can be due to one or more climatic parameters, different from those that were reconstructed. The comparison of the modern distribution of the species and those of climatic parameters might help solve this problem. Thus, improving the steplike variations would be more difficult. Consequently, the use of weighted SCRs, from the climatic data set or from the relative abundance of species, in the calculations of the most probable thermal values of the MCR would probably allow the reconstruction of more extreme, and realistic, temperatures during cold periods.

A third hypothesis takes into account that mollusks can be in dormancy during winter and summer, buried in the soil or under rocks, or settled on plants. Indeed, although the whole geographic distributions of beetle species have been used in the MCR method since its first application (Atkinson *et al*., 1986), the bias persists. Elias (1997) hypothesized that this could be due to the dormancy period of species, so the significance of the extreme temperatures of some SCR appears not to be always directly related to mollusks physiology. Unless the whole geographic distribution of terrestrial mollusks species is known, at present we cannot specify how important the dormancy on climatic reconstructions is.

A fourth hypothesis is that the presence of certain species in a sample could be due to favorable local environmental characteristics other than regional climate. If the allochthonous species are directly linked to ecological climatic characteristics different from those of the sample region, this will lead to biased reconstructions.

The maps of the malacological atlas of Kerney *et al.* (1983) have been interpolated through the location of both field and collection samples. The presence of species may have been assigned to certain regions where they were never sampled, and vice versa. This can then modify the SCR, the MCR, and hence the values reconstructed, especially if the regions, missing or incorrectly assigned, present important magnitudes of parameter values. To avoid these problems, a joint effort should be made between the mapping of present-day malacological distributions and those collecting fossil mollusk samples and their related temperatures.

Comparison between Analogues and MCR Methods

The general trends of the curves of the two methods are similar for the last climatic cycle, but differences remain (Fig. 6). Between 17 and 15 m depth, the analogue curves show strong variations that are not described by using MCR. Between 13 and 8 m depth, variations in the analogue curves show an increase followed by a decrease, whereas the MCR curves show the same variations but separated by a step. This scheme is repeated between 8 and 6 m depth, except that there is no increase at the beginning of this cycle for the MCR $T_{\max}$ curve. During the coldest stage, between 6 and 1 m depth, the thermal minima and maxima of both $T_{\min}$ curves are located at the same depth (except at 4 m); the corresponding values for the MCR curve are higher than those for the analogue method, mainly at the minima. During the same cold stage, the $T_{\max}$ curves are in phase, except between 2.5 and 1 m, with minimal values of the MCR curves generally lower than those of the analogues. Between 1 and 0 m, where the analogue curves show a constant increase of temperature, the MCR curves describe an increase followed by a decrease in temperature.

The analogue minimal temperature curve has a greater variability than its corresponding MCR, mainly in the coldest stage. This lack of variability could come from the "incomplete" SCRs only defined from western and central European distributions; these do not include climatic conditions similar to the last glacial maximum. Lack of variability could also be partially induced by the nonuse of the number of individuals of a species. Thus reconstructed minimum temperatures from the MCR are milder than what could be expected. For the maximum temperature, opposite variability comes from the data-set itself. Indeed there is a linear correlation between $T_{\min}$ and T_{range} ($r^2 = 0.8$). Consequently, weak $T_{\min}$ is associated with high T_{range}. As variations of $T_{\min}$ in several assemblages are smaller than associated variations of T_{range}, this implies strong variability in the $T_{\max}$ curve reconstructed with the MCR method. Differences of variability between the two methods could also come from the estimation of the most probable value, as previously mentioned. The steps present on the curves of the MCR reconstruction are due to equivalent assemblage composition, whose number of individuals in a species could not be used to differentiate them. Some small differences of variation remain unexplained, such as those between 17 and 15 m depth. For the analogue curves, they might be related to the number of species with equivalent variations. The calculation of the correlation coefficient between reconstructed $T_{\min}$ and $T_{\max}$ and the number of individuals of *Pupilla muscorum*, *Succinea oblonga*, and *Trichia hispida* (numerous individuals in assemblages) did not reveal a strong influence of these well-represented species on the reconstruction of the climatic parameters with the MCR. Thus, these differences between the two methods of reconstruction remain unexplained.

CONCLUSION

Among the different thermal factors tested here, the mean temperature of the coldest month and the annual thermal range are the most constraining parameters on the geographic distribution of terrestrial mollusks species. However, the impact of other parameters on species distributions, such as humidity or evapotranspiration, remains to be tested. This requires more appropriate meteorological databases than those currently used. The interaction of different climatic and biological parameters must not be neglected.

The first application of the MCR method to modern terrestrial mollusk assemblages yields thermal values close to the measured ones. We find that the MCR method applied to gastropods is therefore an appropriate and reliable tool for reconstructing seasonal temperature; other climatic parameters shall be incorporated in the future. A bias has been noted, between modern estimated and measured temperatures and is similar to the differences determined when the same method is applied to beetle assemblages. Complementary studies are necessary to confirm the methodological or biological origin of this bias.

The results produced from the application of the MCR method to fossil mollusk assemblages confirm its usefulness in yielding a proxy temperature record for the Late Pleistocene. Nevertheless, problems of reduced variability in the climate signal and of reaching the coldest temperatures have been recognized. Improvement of the transfer function by using the number of individuals or the weighted SCR should help to reduce methodological and ecological problems.

These results obtained on recent and fossil European mollusk assemblages, indicate that the MCR method can be safely applied to terrestrial gastropods to reconstruct variations of past climatic parameters. Continued development of the MCR method for terrestrial mollusks assemblages will make it a vital tool in the climate reconstruction of Quaternary sequences worldwide.

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