# Rodents and climate: A new model for estimating past temperatures

Serge Legendre[a],*, Sophie Montuire[b], Olivier Maridet[a], Gilles Escarguel[a]

[a]UMR CNRS 5125 "Paléoenvironnements et Paléobiosphère", Université Claude Bernard-Lyon 1, Bât. Géode,
  Domaine scientifique de La Doua, F-69622 Villeurbanne Cedex, France
[b]UMR CNRS 5561 Biogéosciences Dijon et Laboratoire EPHE, Centre des Sciences de la Terre,
  Université de Bourgogne, 6 Bld Gabriel, F-21000 Dijon, France

### Abstract

Based on the high correlation between species richness in sigmodontine rodents and temperatures, we propose a new model in order to quantify past climates. Because of the close phylogenetic relationship and the tooth morphological similarity between extant New World cricetids (Sigmodontinae) and fossil European cricetids (Cricetinae s.l.), extant New World sigmodontines are taken as analogues for Old World fossil cricetines. Sigmodontine species richness has been compiled for 282 extant local faunas from North, Central and South America, with corresponding climatic data (temperatures and precipitations). There is almost no correlation between areas covered by local faunas (ranging from 1 km$^2$ up to 46,000 km$^2$) and numbers of sigmodontine species in localities ($R^2 = 0.027$). Number of sigmodontine species in local faunas and mean annual daily temperatures are highly correlated ($R^2 = 0.88$). The relationships of species richness and precipitation is low ($R^2 = 0.19$ for mean annual precipitation).

The method is exemplified for Old World cricetines using well documented Miocene rodent faunas located in the Lyon area (France MN4-5 to MN10).

*Keywords:* palaeoclimatology; air temperature; Neogene; Europe; Rodentia

## 1. Introduction

More and increasingly varied palaeoecological research has been done to determine the past climatic modes. It focuses on several approaches like geochemical proxies (e.g., on vertebrate bones and teeth [1–6]), pollen data [7,8], insects such as coleopterans [9], molluscs [10–12] and mammals (e.g., for rodents [13–17]). Among all these approaches, the study of mammalian faunas has widely contributed to the knowledge of palaeoenvironments and climatic dynamics. Such studies are usually based on analyses of diversity or species richness [18–23], rodent associations [24,25], rodent tooth morphology [26] or mammalian communities [27–31].

* Corresponding author.
  *E-mail address:* Serge.Legendre@univ-lyon1.fr

Biodiversity dynamics, especially in some rodent groups, has been used to reconstruct climatic parameters, mainly temperatures. Two models of biodiversity dynamics that are based on arvicolines and on murines were used to estimate mean air temperatures [21,32–34]. These two models are complementary in time and space. The arvicolines are powerful tools in resolving this climatic parameter for Quaternary sequences from the Palearctic and Nearctic Realms, and the murines since the late Miocene in the Old World. Both subfamilies are rare or absent in older Miocene faunas, which are dominated by cricetines in Europe and western Asia.

Present-day cricetines are confined to Eurasia, living in steppic environments [35]. They are restricted to 7 genera compared to more than 30 genera in European faunas since the Oligocene. In contrast, the sigmodontines, a New World murid subfamily closely related to the cricetines, are represented by about 100 genera in North, Central and South America [35]. By comparing the fossil genera *Democricetodon* (a well known middle Miocene European genus) and *Copemys* from America (leading to modern *Peromyscus*) Fahlbusch [36] suggested that the European cricetid genus *Democricetodon* may be the ancestor of some of the American deer mice. Engesser [37] compared *Democricetodon* with *Copemys* and *Eumyarion* (Europe) with *Leidymys* (North America) and reached a similar conclusion, i.e., a high affinity between New World sigmodontines and Old World cricetines. Several other authors (e.g., [38,39]) discussed the relationships between New World cricetids (here, sigmodontines) and Old World muroids. Dental morphologies within extant sigmodontines are very close to those observed in Neogene European cricetines [40,41], and the range in body size of both groups is very similar, approximately from 10 to 300 g [42]. The similarity between European fossil cricetine rodents and modern sigmodontines allows the use of the New World subfamily as an ecological analogue for European fossil cricetids.

The method is exemplified for Old World cricetines using well documented Miocene rodent faunas located in the Lyon area (France; MN4-5 to MN10). The method was applied to a larger fossil dataset elsewhere [43].

## 2. The Sigmodontinae

The Sigmodontinae (Muridae, Rodentia sensu Musser and Carleton in Wilson and Reeder [44]) correspond to the New World rats and mice. The oldest sigmodontines are recorded from the late Miocene of North America. Eleven tribes are described in this sub-family (Table 1), which is composed of 12 fossil genera and 84 present-day genera [45] and more than 300 species occupying a wide variety of niches: from hopping mice to semi-aquatic swimmers that hunt fish and crustaceans. They can be found at altitude of over 5000 m high in the Andes. The centers of diversity are now in South America, but many species can be found in Central America and some species occur as far North as the Central United States.

Extant species systematics are based on Musser and Carleton [35]. Thus, cricetines in this paper correspond to cricetids from the authors dealing with European fossil rodents (as, for example: [46,47]).

Table 1
List of sigmodontine tribes, with temporal and geographical ranges (after [45])

| Tribe | Temporal range | Geographical range |
|---|---|---|
| Tylomyini | Recent | Mexico, Central and South America |
| Neotomini | Late Miocene–recent | North America |
| | Recent | South America |
| Peromyscini | Late Miocene–recent | North America |
| | Recent | Central and South America |
| Oryzomyini | Possibly Late Miocene | North America |
| | Late Pleistocene–recent | North America |
| | Pleistocene–recent | South America |
| | Recent | Central America |
| Thomasomyini | Pleistocene–recent | South America |
| | Recent | Central America in Panama |
| Wiedomyini | Early Pleistocene–recent | South America |
| Akodontini | Late Pliocene–recent | South America |
| Phyllotini | Late Pliocene–recent | South America |
| Sigmodontini | Early Pliocene–recent | North America |
| | Recent | Central and South America |
| Scapteromyini | Late Pliocene–recent | South America |
| Ichthyomyini | Recent | North, Central and South America |

## 3. Data used and method

### 3.1. Extant species data

Species lists for sigmodontines were compiled for extant local faunas in the New World (Fig. 1) using three main sources (given in order of preference): (1) published faunas resulting from local faunistic studies, (2) local faunas extracted from regional mammalogical distribution and systematic monographs, and (3) lists of mammalian species for protected areas (National or Provincial Parks, Wildlife Reserve, Recreation Areas, etc.) in several countries provided by the Information Center for the Environment, University of California in Davis (http://ice.ucdavis.edu/). When local faunas were established from monographs, as far as possible, only attested presence of a species (as specimens in Museum collections or any activity tracks) within the defined area was taken into account. The distribution range of a species was used only when the gazetteer of its observed specimens was not available.

The 282 extant local faunas correspond to areas varying from 1–2 km$^2$ up to 46,000 km$^2$, but only 13 localities represent areas greater than or equal to 10,000 km$^2$. The median is about 450 km$^2$. Larger areas occur most of the time in northern high latitudes.
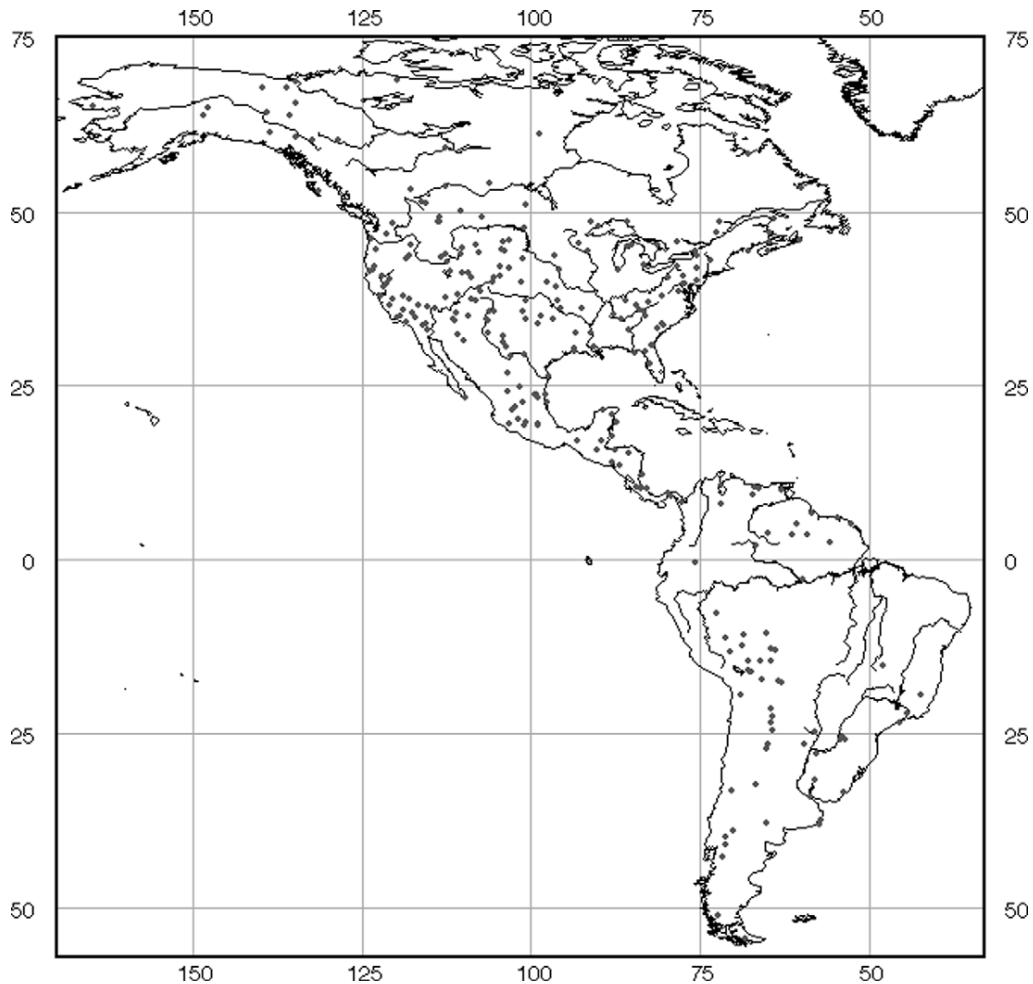


Fig. 1. Geographical location of the extant faunas used in this study (detailed data available upon request as an electronic supplement).

### 3.2. Climatic data

Climatic parameters are mean annual daily temperatures, mean daily temperatures of the coldest (minimum) and warmest (maximum) month, and annual precipitation. They are taken from Wernstedt [48] and from the Global Climate Perspectives System database (NOAA, National Climatic Data Center; http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/). They are combined with local data, when available in specific studies.

Geographical and climatic data, and the list of sigmodontine species are available upon request as an electronic supplement.

### 3.3. Fossil data

In order to illustrate the method applied to fossil western European cricetine data, we used several localities from the French East-Central area, in the vicinity of Lyon. All the localities are dated between the Middle and the Late Miocene, MN4–MN10, using the mammalian biochronological continental time scale [49–51].

The oldest locality is Vieux-Collonges [52–55] and it is dated from the end of MN4 [49]. Isle d'Abeau droite is a new unpublished locality (P. Mein, pers. comm.) distinct from the Isle d'Abeau faunal list provided by Guérin and Mein [53] and later mentioned by Mein [56]. It is younger than Vieux-Collonges, and it is dated within the MN5 biochro-nological unit. La Grive M is the reference locality for the MN7/8 unit [49] and its fauna is close to that of La Grive L7 [56–58], nevertheless La Grive L7 is slightly older than La Grive M. CD24 is a new karstic locality, older than La Grive M and closely related to the lowermost layer of the fissure filling at Four, dated from the end of MN 6 unit or the very beginning of MN7/8 unit [59,60]. The fauna of La Grive L3 [56,61] differs from that of La Grive M and La Grive L7. This locality is thus considered as younger than CD24, La Grive M and La Grive L7, and is probably close to the end of the MN7/8 unit. Jujurieux [62] is a late Miocene locality from the Lyon area, and it is placed in the MN9 unit. The last locality dated from the MN10 unit, Soblay [62], bears the first murine rodents linked to the decrease of cricetines in European faunas. Except for Jujurieux and Soblay, localities are karstic deposits.

The list of cricetines for fossil localities is provided in the Appendix. Table 2 summarizes fossil data, with an approximate numerical age, the number of cricetine species available for each locality, and the total number of rodent species. This rodent species number demonstrates that there is no link between decrease in cricetid richness and neither the type of deposit (karst or bedded sediment) nor the overall quality of the sample. Deposit types influence the relative species abundance more than their presence–absence and the heterogeneity of the preservation of several parts of individuals [64,65].

Table 2

List of Miocene localities from East-Central France used to exemplify the method using sigmodontine rodents for predicting past temperatures

| Locality | MN Zone | Estimated age (m.a.) | | N cri. | N rod. | Type | References |
|---|---|---|---|---|---|---|---|
| | | (1) | (2) | | | | |
| Vieux-Collonges | MN4–MN5 boundary | 16.1–15.7 | 16.1–15.3 | 15 | 42 | K | [52–55] |
| Isle d'Abeau droite | Early MN5 | 16.0–14.8 | 16.0–14.8 | 8 | 15 | K | Unpublished, P. Mein, pers. comm. |
| CD 24 | Late MN 6–early MN7/8 | 13.0–12.0 | 14.5–13.5 | 8 | 14 | K | [58,60] |
| La Grive L7 | Early MN7/8 | 12.5–12.1 | 14.0–13.6 | 10 | 28 | K | [58] |
| La Grive M | Early MN7/8 | 12.4–12.0 | 13.9–13.5 | 11 | 25 | K | [58] |
| La Grive L3 | Late MN7/8 | 12.0–11.5 | 13.5–13.0 | 10 | 17 | K | [58] |
| Jujurieux | MN9 | 11.1–9.7 | 11.8–11,6 | 5 | 14 | S | [62,75] |
| Soblay | MN10 | 9.7–8.7 | 9.7–8.7 | 4 | 20 | S | [62] |

Numerical ages are based (1) on Neogene mammal scale calibration [51] with global MPTS [63] and (2) on a shift to 1.5 m.a. older values between MN6 and MN9 based on [73–75] (see text for explanations). Abbreviations: N cri., number of cricetid species; N rod., total number of rodent species; K, karst deposit; S, stratified deposit.

## 3.4. Method

The principle of this method is based on the log–log linear relationship between sigmodontine rodent richness and climatic data in the Present for Old World fossil cricetines, inasmuch as cricetines are considered as analogous to the New World sigmodontines.

For species richness, we used $\log_{10}(N+1)$, where $N$ is the number of sigmodontine (or cricetine) species in a local fauna. Due to possible negative values, air temperature values are transformed in Kelvin for calculations, i.e., $\log_{10}(\theta+273.15)$, where $\theta$ is the temperature in Celsius. For precipitation, the values entered in the calculation were $\log_{10}(P+1)$, where $P$ is the precipitation amount in millimeters.

The method used was linear least square regression (e.g. [66–68]), with species richness as the independent variable ($=X$) and climatic parameter as the dependent one ($=Y$), as it was previously processed for arvicolines [21] and for murines [34].

A robust regression technique, the least median of squares regression (LMS; [69]), has been carried out in order to detect outliers. We used the latest version of the program PROGRESS [70], with a breakdown value of 25% (for detailed explanation on the LMS regression and PROGRESS, see [69]).

## 4. Results: regression analysis of extant data

First of all, the data set was checked for independency between the number of sigmodontine rodents and locality areas (Fig. 2; $R^2=0.027$, $p=0.005$), which means that the number of species was not controlled by the geographical area covered by the fauna. Climatic parameters and species richness in extant fauna were reported as bivariate plots (Figs. 3-6).

For mean annual temperatures (Fig. 3), the determination coefficient is high ($R^2=0.798$, $p<0.0001$). The regression line has a slope of 0.0409, an intercept of 2.4257 with a mean standard error of the estimates equal to 0.0060. When applying outlier detection with least median of squares regression [69], three kinds of faunas (open symbols in Fig. 3) occur outside of the main distribution (black circles in Fig. 3):

1) Southern Andean National Parks (Lanín NP, Nahuel Huapi NP, Torres del Paine NP, Terra del Fuego NP; open circles in Fig. 3) are characterized by a high diversity of species for lower temperatures and they cover large areas made up of contrasting habitats from low elevations up to Alpine ecosystems,
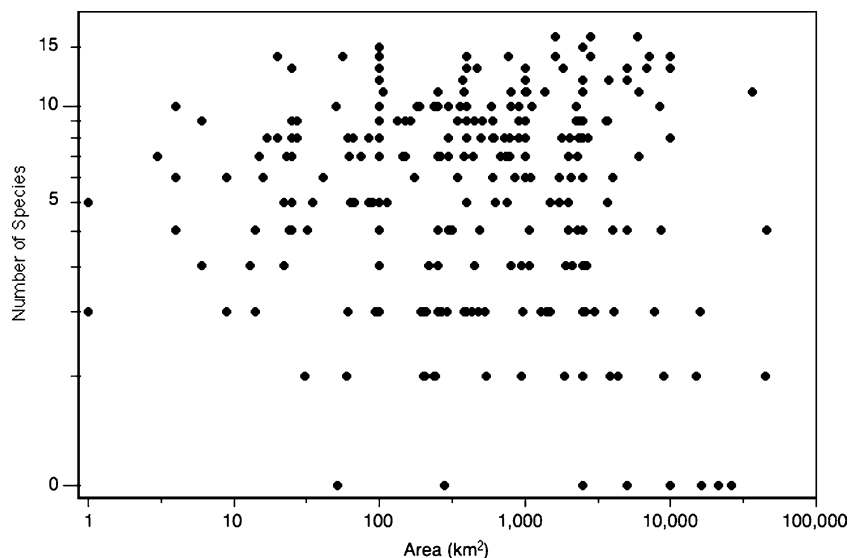


Fig. 2. Scatter diagram of the number of sigmodontine species and the area. Species richness is statistically independent from the geographical area in our dataset ($N=282$, $R^2=0.027$).
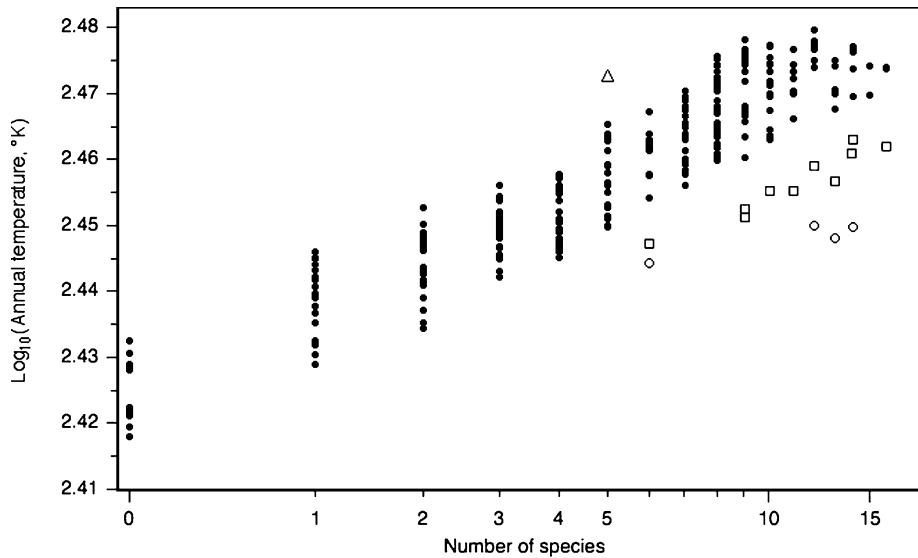
Fig. 3. Number of sigmodontine species vs. mean annual daily temperature ($N=261$, $R^2=0.882$). Faunas in open symbols represent faunas with abnormal number of species and are considered as outliers (see text for explanations).

2) Cabo (open triangle in Fig. 3), located at the head of the very narrow peninsula of Baja California in Mexico, is characterized by a low species diversity,

3) Localities in the southern part of the Rocky Mountains in the United States (Arizona, Colorado, New Mexico, Texas; open squares in Fig. 3) have a high

sigmodontine richness despite a very similar slope for the regression line ($R^2=0.915$, $N=10$, $p<0.0001$; slope=$0.04218 \pm 0.00456$).

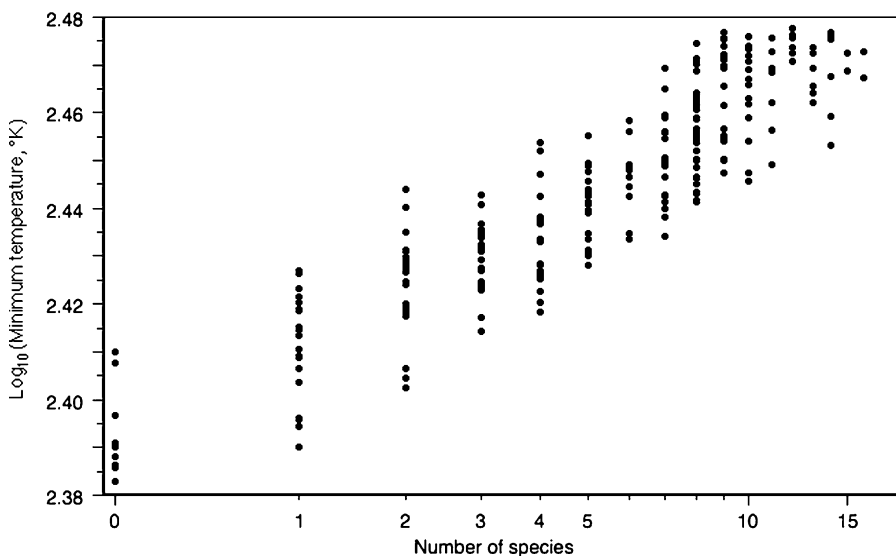All these localities are thereafter considered as outliers and they are excluded from the subsequent calcu-



Fig. 4. Number of sigmodontine species vs. mean daily temperature of the coldest month ($N=261$, $R^2=0.835$). Faunas considered as outliers in Fig. 3 are omitted.
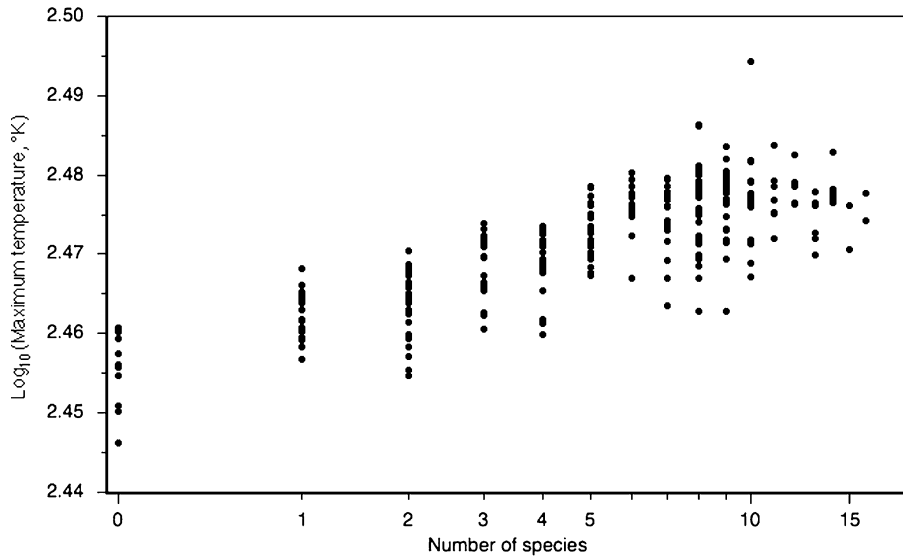
Fig. 5. Number of sigmodontine species vs. mean daily temperature of the warmest month ($N=261$, $R^2=0.643$). Faunas considered as outliers in Fig. 3 are omitted.

lations. The parameters of each bivariate regression analysis between sigmodontine species richness (without the faunas considered as outliers) and the four climatic parameters are given in Table 3. The correlations between species richness and mean annual tem-perature (Fig. 3; $R^2=0.882$, $N=261$, $p<0.0001$) is much higher than that with annual precipitation (Fig. 6; $R^2=0.193$, $N=267$, $p<0.0001$). Annual temperature is better correlated to the number of sigmodontine species ($R^2=0.882$) than the mean daily temperature
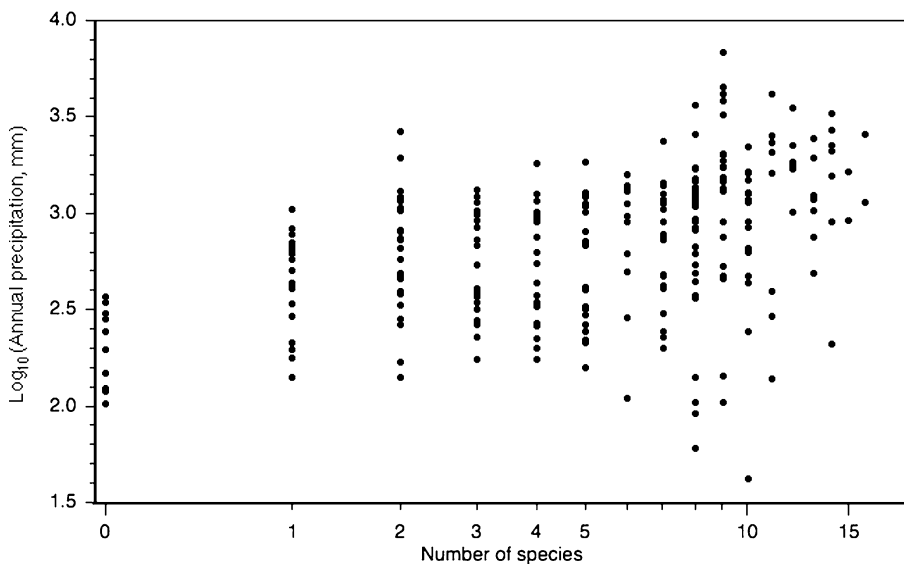


Fig. 6. Number of sigmodontine species vs. annual precipitation ($N=267$, $R^2=0.193$). Faunas considered as outliers in Fig. 3 are omitted.

Table 3
Regression statistics for least square analysis between climatic parameters and number of sigmodontine species

|  | $N$ | $R^2$ | Slope $\pm$ SE | Intercept $\pm$ SE | SE estim. |
|---|---|---|---|---|---|
| Annual temperature | 261 | 0.8820 | $0.04395 \pm 0.00100$ | $2.42411 \pm 0.00083$ | 0.00472 |
| Minimum temperature | 261 | 0.8352 | $0.06969 \pm 0.00192$ | $2.38960 \pm 0.00159$ | 0.00908 |
| Maximum temperature | 261 | 0.6432 | $0.02011 \pm 0.00093$ | $2.45601 \pm 0.00077$ | 0.00439 |
| Annual precipitation | 267 | 0.1930 | $0.56923 \pm 0.07150$ | $2.40568 \pm 0.05955$ | 0.34061 |

Outliers are omitted from calculation (see text and Fig. 3).

of the coldest month (Fig. 4; $R^2 = 0.835$, $N = 261$, $p < 0.0001$), whereas the mean daily temperature of the warmest month is less correlated to the species number (Fig. 5; $R^2 = 0.643$, $N = 261$, $p < 0.0001$).

## 5. Climatic predictions for fossil faunas

The regression parameters obtained from the preceding analysis can be used for predicting temperature values derived from fossil sigmodontine assemblages. The predicted temperature for each $N$ value ranging from 0 to 20, along with the statistical prediction error, are given in Table 4. As

explained in the introduction, we used sigmodontines as analogues to fossil cricetines. In order to exemplify the method, we apply the prediction equations to fossil faunas from East-Central France. The results are given in Table 5 and are illustrated in Fig. 7.

Predicted temperatures using present New World sigmodontine rodents as analogues to European Neogene cricetines are consistent and they are within the range of the observed extant values. The main observation that is retrievable from these estimates is the drastic drop in temperatures between the MN7/8 and the MN9 units, i.e. at approximately 12 My. (Fig. 7A): mean annual temperatures decreased in

Table 4
Predicted temperature values for number of sigmodontine and cricetine species varying from 0 to 20, with prediction standard error

| N Sp. | Annual $\pm$ SE | Minimum $\pm$ SE | Maximum $\pm$ SE | Annual (°C) | Minimum (°C) | Maximum (°C) |
|---|---|---|---|---|---|---|
| 0 | $2.424113 \pm 0.004787$ | $2.389599 \pm 0.009220$ | $2.456009 \pm 0.004461$ | $-7.6 \,(-10.5/-4.7)$ | $-27.9 \,(-33.1/-22.6)$ | $12.6 \,(9.7/15.6)$ |
| 1 | $2.437345 \pm 0.004748$ | $2.410577 \pm 0.009144$ | $2.462063 \pm 0.004424$ | $0.6 \,(-2.4/3.6)$ | $-15.8 \,(-21.1/-10.3)$ | $16.6 \,(13.7/19.6)$ |
| 2 | $2.445084 \pm 0.004734$ | $2.422848 \pm 0.009117$ | $2.465604 \pm 0.004411$ | $5.5 \,(2.5/8.6)$ | $-8.4 \,(-13.9/-2.8)$ | $19.0 \,(16.0/22.0)$ |
| 3 | $2.450576 \pm 0.004727$ | $2.431554 \pm 0.009105$ | $2.468117 \pm 0.004405$ | $9.1 \,(6.0/12.2)$ | $-3.0 \,(-8.6/2.7)$ | $20.7 \,(17.7/23.7)$ |
| 4 | $2.454836 \pm 0.004725$ | $2.438308 \pm 0.009100$ | $2.470066 \pm 0.004403$ | $11.8 \,(8.8/15.0)$ | $1.2 \,(-4.5/7.0)$ | $22.0 \,(19.0/25.0)$ |
| 5 | $2.458316 \pm 0.004724$ | $2.443826 \pm 0.009099$ | $2.471658 \pm 0.004402$ | $14.1 \,(11.0/17.3)$ | $4.7 \,(-1.1/10.6)$ | $23.1 \,(20.1/26.1)$ |
| 6 | $2.461258 \pm 0.004725$ | $2.448491 \pm 0.009100$ | $2.473004 \pm 0.004403$ | $16.1 \,(13.0/19.3)$ | $7.7 \,(1.9/13.7)$ | $24.0 \,(21.0/27.0)$ |
| 7 | $2.463807 \pm 0.004726$ | $2.452532 \pm 0.009102$ | $2.474171 \pm 0.004404$ | $17.8 \,(14.6/21.0)$ | $10.3 \,(4.5/16.3)$ | $24.8 \,(21.8/27.9)$ |
| 8 | $2.466056 \pm 0.004728$ | $2.456097 \pm 0.009105$ | $2.475199 \pm 0.004405$ | $19.3 \,(16.1/22.5)$ | $12.7 \,(6.7/18.7)$ | $25.5 \,(22.5/28.6)$ |
| 9 | $2.468067 \pm 0.004730$ | $2.459286 \pm 0.009109$ | $2.476120 \pm 0.004407$ | $20.7 \,(17.5/23.9)$ | $14.8 \,(8.8/20.9)$ | $26.2 \,(23.1/29.2)$ |
| 10 | $2.469886 \pm 0.004732$ | $2.462170 \pm 0.009113$ | $2.476952 \pm 0.004409$ | $21.9 \,(18.7/25.1)$ | $16.7 \,(10.7/22.8)$ | $26.7 \,(23.7/29.8)$ |
| 11 | $2.471547 \pm 0.004734$ | $2.464804 \pm 0.009118$ | $2.477712 \pm 0.004411$ | $23.0 \,(19.8/26.3)$ | $18.5 \,(12.4/24.6)$ | $27.3 \,(24.2/30.3)$ |
| 12 | $2.473075 \pm 0.004736$ | $2.467226 \pm 0.009122$ | $2.478411 \pm 0.004414$ | $24.1 \,(20.8/27.3)$ | $20.1 \,(14.0/26.3)$ | $27.7 \,(24.7/30.8)$ |
| 13 | $2.474490 \pm 0.004739$ | $2.469469 \pm 0.009127$ | $2.479058 \pm 0.004416$ | $25.0 \,(21.8/28.3)$ | $21.6 \,(15.5/27.9)$ | $28.2 \,(25.1/31.3)$ |
| 14 | $2.475807 \pm 0.004741$ | $2.471557 \pm 0.009131$ | $2.479661 \pm 0.004418$ | $25.9 \,(22.7/29.2)$ | $23.0 \,(16.9/29.3)$ | $28.6 \,(25.6/31.7)$ |
| 15 | $2.477039 \pm 0.004744$ | $2.473510 \pm 0.009136$ | $2.480225 \pm 0.004420$ | $26.8 \,(23.5/30.1)$ | $24.4 \,(18.2/30.7)$ | $29.0 \,(25.9/32.1)$ |
| 16 | $2.478196 \pm 0.004746$ | $2.475345 \pm 0.009141$ | $2.480754 \pm 0.004423$ | $27.6 \,(24.3/30.9)$ | $25.6 \,(19.4/32.0)$ | $29.4 \,(26.3/32.5)$ |
| 17 | $2.479287 \pm 0.004749$ | $2.477075 \pm 0.009146$ | $2.481253 \pm 0.004425$ | $28.3 \,(25.1/31.7)$ | $26.8 \,(20.6/33.2)$ | $29.7 \,(26.6/32.8)$ |
| 18 | $2.480319 \pm 0.004751$ | $2.478711 \pm 0.009150$ | $2.481725 \pm 0.004427$ | $29.1 \,(25.8/32.4)$ | $28.0 \,(21.7/34.4)$ | $30.0 \,(27.0/33.2)$ |
| 19 | $2.481298 \pm 0.004753$ | $2.480263 \pm 0.009155$ | $2.482173 \pm 0.004429$ | $29.7 \,(26.5/33.1)$ | $29.0 \,(22.7/35.5)$ | $30.4 \,(27.3/33.5)$ |
| 20 | $2.482230 \pm 0.004756$ | $2.481740 \pm 0.009159$ | $2.482600 \pm 0.004432$ | $30.4 \,(27.1/33.7)$ | $30.1 \,(23.7/36.5)$ | $30.7 \,(27.6/33.8)$ |

The calculations are in $\log_{10}$ of $N+1$ and of temperature in Kelvin. Temperature values in Celsius and confident interval for 1 prediction standard error (SE) are provided in the 3 right hand columns.

Table 5
Temperature predictions, with confidence interval as provided in Table 4, for middle Miocene faunas from East-Central France (see Table 2 for details)

| Locality | N sp. | Annual (°C) | Minimum (°C) | Maximum (°C) |
|---|---|---|---|---|
| Vieux-Collonges | 15 | 26.8 (23.5/30.1) | 24.4 (18.2/30.7) | 29.0 (25.9/32.1) |
| Isle d'Abeau droite | 8 | 19.3 (16.1/22.5) | 12.7 (6.7/18.7) | 25.5 (22.5/28.6) |
| CD 24 | 8 | 19.3 (16.1/22.5) | 12.7 (6.7/18.7) | 25.5 (22.5/28.6) |
| La Grive L7 | 10 | 21.9 (18.7/25.1) | 16.7 (10.7/22.8) | 26.7 (23.7/29.8) |
| La Grive M | 11 | 23.0 (19.8/26.3) | 18.5 (12.4/24.6) | 27.3 (24.2/30.3) |
| La Grive L3 | 10 | 21.9 (18.7/25.1) | 16.7 (10.7/22.8) | 26.7 (23.7/29.8) |
| Jujurieux | 5 | 14.1 (11.0/17.3) | 4.7 (−1.1/10.6) | 23.1 (20.1/26.1) |
| Soblay | 4 | 11.8 (8.8/15.0) | 1.2 (−4.5/7.0) | 22.0 (19.0/25.0) |

the range 7–9 °C. In the ocean, a major shift in global $\delta^{18}O$ values of planktonic foraminifera appeared during the Middle Miocene (e.g., Atlantic DSDP site 608; [71]) and is known as the mid-Miocene event. This isotopic shift, associated with the Monterey Event [72], is dated between 13.5 and 13 My. If both continental temperature drop and major marine $\delta^{18}O$ shift were not contemporaneous, they are however coincident enough to most likely represent a response to a unique global event. The temporal discrepancy for this event can result from a lagged response in terrestrial ecosystems in comparison with marine ones, or from a correlation problem intrinsic to the European continental biochronological time scale. This last hypothesis (Fig. 7B) is reinforced by recent results, which suggested that

some MN zone limits must be older than believed: (1) Sen [73] and Sen and Ginsburg [74] proposed an age not younger than 15 My for Sansan, the type locality for MN6, i.e. about 1.5 My older than generally accepted; and (2) Aguilar et al. [75] proposed an age of 11.5 My for Can Llobateres, the reference fauna for MN9, i.e. ca. 2 My older than previously proposed [51].

## 6. Conclusions

The method for predicting past climate based on sigmodontine rodents is not only powerful when applied to fossil New World sigmodontine faunas but also to fossil European and Asian cricetid faunas. The
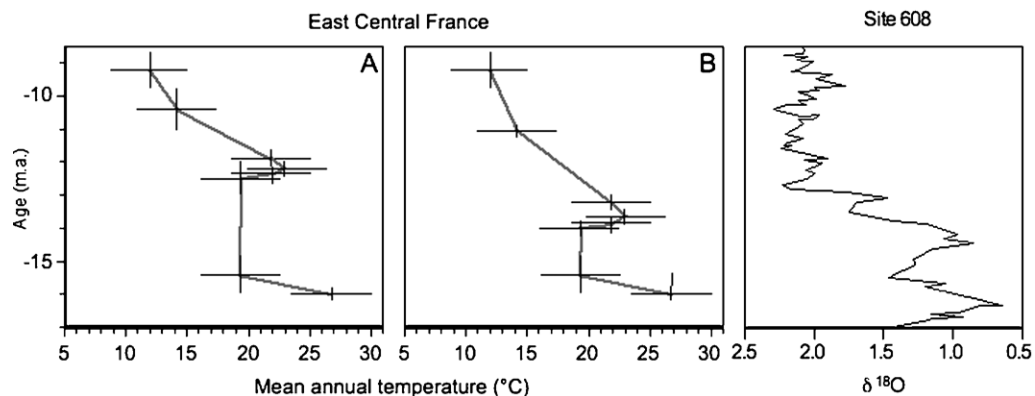


Fig. 7. Mean annual temperature reconstruction for fossil faunas from East-Central France area (A and B; see Tables 2 and 5 for details) and oxygen isotope curve based on planktonic foraminifera (site 608, North Atlantic; [71]). Numerical ages of localities based (A) on [51] and (B) on [73–75] (see text for explanation).

highest relationship with species richness is for mean annual temperature, and, to a lesser degree, for monthly minimum temperature, whereas it is lower for monthly maximum temperature. However, a weak correlation between present day distribution of sigmodontine species and precipitation precludes its use for rainfall estimates.

The species richness of Miocene cricetid faunas from East-Central France suggests a temperature drop of about 7–9 °C in continental Europe at about 12 My (based on calibration proposed in [51]) or at 13.5–13 (based on [73–75]), which must be tested by other approaches such as pollen analysis or oxygen isotope composition of mammalian tooth apatite.

Finally, this method based on sigmodontine rodents complements those based on other murid subfamilies, the arvicolines [21] and the murines [34]. It expands temporally and geographically the use of rodents for estimating past air temperatures. Whilst arvicolines are useful for late Pliocene and Quaternary Palearctic sequences and murines for Old World since the late Miocene, crictetines in the Old World and sigmodontines in the New World represent a significant component of rodent faunas since the beginning of the Oligocene, a time when these murid subfamilies radiated. Thus, the method presented in this study can be applied to post-Eocene faunas, when species richness within this subfamily is not regionally altered by peculiar biogeographical or climatic conditions.

## Acknowledgements

## Appendix A. List of cricetine (s.l.) species in fossil localities from East-Central France used in this study

Vieux-Collonges [52–55]: *Anomalomys minor*, *Cricetodon aureus*, *C. meini*, *Democricetodon mutilus*, *D.* sp., *Eumyarion bifidus*, *E. weinfurteri*, *Fahlbuschia darocensis*, *Lartetomys mirabilis*, *L. zapfei*, *Megacricetodon bourgeoisi*, *M. collongensis*, *M. lappi*, *Melissiodon dominans*, *Neocometes similis*.

Isle d'Abeau droite (unpublished, P. Mein, pers. comm.): *Democricetodon* aff. *freisingensis*, *D. brevis*, *D.* cf. *mutilus*, *Eumyarion bifidus*, *E. weinfurteri*, *Megacricetodon germanicus*, *M. minor*, *Neocometes brunonis*.

La Grive L7 [58]: *Anomalomys gaudryi*, *Cricetodon albanensis*, *C.* cf. *jotae*, *Democricetodon* aff. *freisingensis*, *D. affinis*, *D. brevis*, *Eumyarion latior*, *Fahlbuschia larteti*, *Megacricetodon gregarius*, *M. minor*.

La Grive M [58]: *Anomalomys gaudryi*, *Cricetodon albanensis*, *Democricetodon* aff. *freisingensis*, *D. affinis*, *D. brevis*, *Eumyarion latior*, *Fahlbuschia larteti*, *F.* sp., *Hispanomys decedens*, *Megacricetodon gregarius*, *M. minor*.

CD 24 [58,60]: *Anomalomys gaudryi*, *Democricetodon* aff. *freisingensis*, *D. brevis*, *D. fourensis*, *Eumyarion latior*, *Megacricetodon* cf. *similis*, *M. gregarius*, *M.* nov. sp.

La Grive L3 [58]: *Anomalomys gaudryi*, *Cricetodon* sp., *Democricetodon* aff. *freisingensis*, *D. affinis*, *D. brevis*, *Eumyarion latior*, *Fahlbuschia* cf. *crusafonti*, *Hispanomys bijugatus*, *Megacricetodon* aff. *ibericus*, *M. minor*.

Jujurieux [62,75]: *Anomalomys* cf. *gaudryi*, *Democricetodon* cf. *nemoralis*, *Eumyarion* cf. *latior*, *Hispanomys bijugatus*, *Megacricetodon* cf. *freudenthali*.

Soblay [61]: *Hispanomys mediterraneus*, *Neocricetodon* cf. *lavocati*, *Prospalax petteri*, *Rotundomys bressanus*.

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