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# A macroecological glance at the structure of late Miocene rodent assemblages from Southwest Europe

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Deep-time perspectives in macroecology are essential with regard to understanding the impact of climate forcing on faunal communities. Using late Miocene rodent faunas (12 to 5 Ma) from two different biogeographical provinces from southwestern Europe, we asked whether the waxing and waning of faunas with dissimilar ecological affinities tracked climate in different ways. The latest middle Miocene featured a fauna dominated by dormice with forest and mixed-habitat affinities. This group declined towards the Upper Miocene. Rodent taxa with the highest values of richness at the beginning of the Upper Miocene are generalists in the southern province and specialists of forested habitats in the northern province. Finally, we identified a third, increasingly significant group of rodents linked to open landscapes towards the end of the Miocene. These three broad ecological groups showed differential responses to a complex set of interconnected circumstances, including the biogeographic structure of the study area and climatic changes throughout time.

Changes in environmental conditions strongly affect the development of faunal communities<sup>1</sup>. Indeed, reciprocal relationships might be operating between organisms and environmental factors<sup>2</sup>. Such relationships can be identified at local and broad scales and affect the structure and function of ecosystems<sup>3,4</sup>.

Research on community ecology has traditionally emphasised the identification of recurrent faunal assemblages at different times and in different places<sup>5</sup>. Based on the idea that faunal communities are non-random sets of species<sup>2</sup>, these ecological studies have focused on the characterization of past communities<sup>6</sup> and the understanding of the patterns of community structure over time.

Furthermore, macroecological studies favour the description of changes in biotic communities related to evolutionary processes or climatic trends through wide spatial<sup>7,8</sup> and —when applied to the fossil record—temporal scales<sup>9</sup>. Thus, deep-time macroecological approaches are critical with regard to investigating the consequences of climatic changes on ancient mammal faunas.

Rodents are a paramount study group within this context because they are ubiquitous, highly diverse and provide detailed palaeoenvironmental information at fine temporal scales<sup>10–12</sup>. Indeed, their rich fossil record has been used to unveil connections between past faunal events and abiotic factors<sup>13,14</sup>.

Herein we focus on the end of the Miocene (12 to 5 Ma), an interval of crucial climate shifts<sup>15,16</sup>, and examine the impact of environmental forcing on the community composition of rodent faunas in the well-known fossil record of southwestern Europe. First, based on the concept of ecological guilds<sup>2</sup> and using Principal Components Analysis (PCA), we ask whether the late Miocene rodent faunas can be grouped according to similar biodiversity patterns throughout time as a result of similar ecological affinities. Subsequently we statistically assess the responses to Miocene climate shifts, testing the correspondence of their evolutionary trends together with a detailed palaeoclimatic proxy.

## Results and Discussion

The PCA produced six significant factors (see the sedimentation graph in the supplementary information Fig. S1) that accounted for more than 60% of the variance. Thus, the late Miocene rodent fossil record can be summarised in six sets of genera with similar patterns of variation within communities, in the present paper called faunal



**Table 1** | Genera included in each faunal component based upon their highest contribution to the PCA factors, according to the components matrix (Supplementary information Tables S1 and S2)

Family	Faunal component					
	I	II	III	IV	V	VI
Sciuridae	<i>Atlantoxerus</i>	<i>Albanensia</i> <i>Blackia</i> <i>Hylometes</i> <i>Miopetaurista</i> <i>Pliopetaurista</i> <i>Tamias</i>	<i>Spermophilinus</i>			<i>Heteroxerus</i> <i>Palaeosciurus</i>
Gliridae	<i>Eliomys</i>	<i>Glirulus</i> <i>Glis</i> <i>Graphiurops</i> <i>Ramys</i>	<i>Tempestia</i>		<i>Bransatoglis</i> <i>Glirudinus</i> <i>Myoglis</i> <i>Eomuscardinus</i> <i>Muscardinus</i> <i>Myomimus</i> <i>Paraglrilulus</i>	<i>Armantomys</i> <i>Microdyromys</i> <i>Miodyromys</i> <i>Pseudodyromys</i>
Castoridae		<i>Chalicomys</i> <i>Palaeomys</i> <i>Trogontherium</i>		<i>Dipoides</i>		
Eomyidae		<i>Eomyops</i> <i>Keramidomys</i> <i>Eozapus</i>				
Dipodidae						
Calomyscidae	<i>Calomyscus</i>					
Nesomyidae	<i>Dendromus</i>					
Cricetidae	<i>Trilophomys</i>	<i>Microtocricetus</i> <i>Cricetulodon</i> <i>Neocricetodon</i> <i>Rotundomys</i>	<i>Hispanomys</i>	<i>Blancomys</i> <i>Ruscinomys</i> <i>Apocricetus</i>	<i>Democricetodon</i> <i>Eumyarion</i>	<i>Cricetodon</i> <i>Megacricetodon</i>
Muridae	<i>Debruijnimys</i> <i>Myocricetodon</i> <i>Pseudomeriones</i> <i>Castillomys</i> <i>Micromys</i> <i>Paraethomys</i> <i>Stephanomys</i>	<i>Epimeriones</i>	<i>Apodemus</i> <i>Huerzelerimys</i> <i>Occitanomys</i> <i>Progonomys</i>	<i>Anthracomys</i> <i>Castromys</i> <i>Rhagapodemus</i>		
Anomalomyidae		<i>Anomalomys</i> <i>Prospalax</i>				
Hystriidae				<i>Hystrix</i>		

components (FC I to IV, see Table 1 and supplementary information Tables S1 and S2). In order to ease the differentiation between PCA factors and faunal components, the former was numbered with Arabic notation and the latter with Roman numerals.

The temporal series of the six PCA factors and the species diversity of their related faunal components in both the northern and southern provinces are represented in Figures 1 and 2 respectively. Herein we assume that the common pattern of such sets of genera over time results from common ecological affinities and similar responses to ecological shifts. Interestingly, our bootstrapping analysis highlights the fact that the sites-per-basin ratio of the northern basin is suitable for a robust macroecological reconstruction (see supplementary information Fig. S2). Geographic differences between provinces regarding diversity patterns are clearly shown in Figure 3.

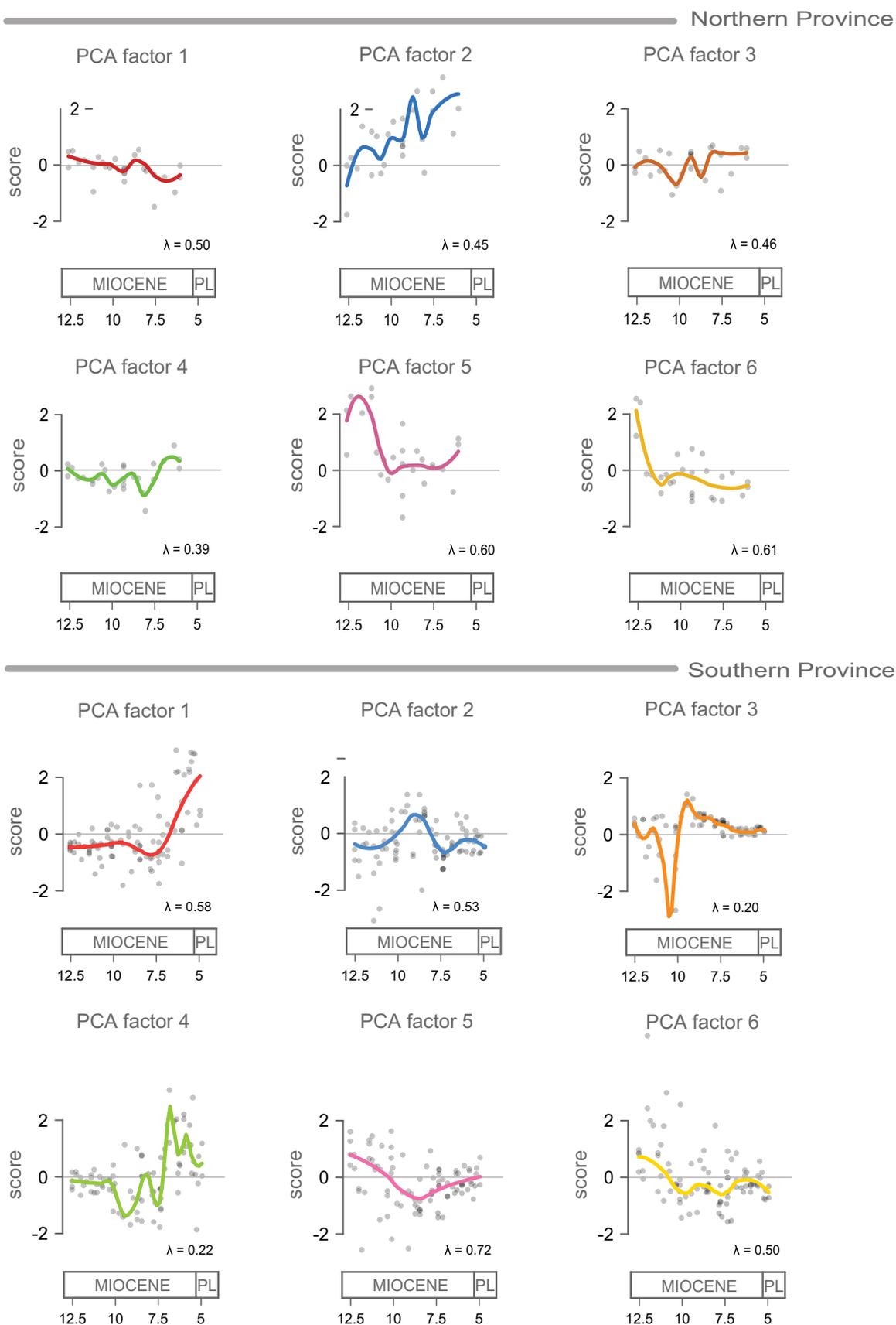
The six FCs can be classified into three groups due to similarities in factor scores and richness patterns throughout time.

Latest middle Miocene faunal components. FC V and FC VI comprise genera with their highest preponderance in the latest Middle Miocene (the oldest time lapse considered in this study) (Fig. 1 and Fig. 2). These two faunal components are mainly dominated by glirids. These, however, show different ecological preferences in each component<sup>17</sup>. Most of the glirids grouped in the faunal component V have classically been considered as forest dwellers due to their brachyodont molars<sup>18</sup>. This is congruent with the fact that the genera grouped in this component are usually more diverse in the northern province (Fig. 2 and Fig. 3), where these taxa found a distinctive

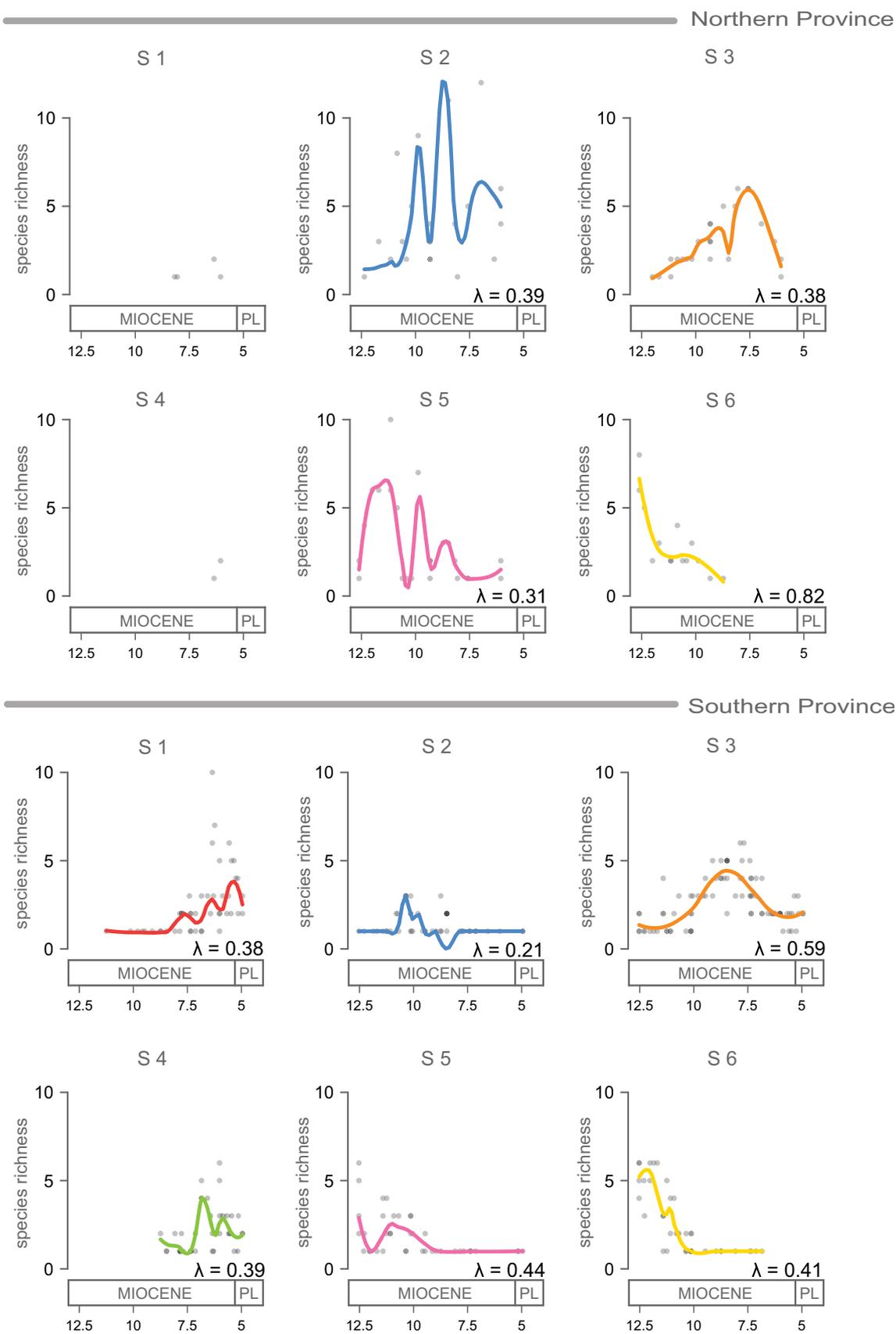
environment, which might have acted as a forest refuge<sup>19,20</sup>. Glirids included in FC VI (e.g. *Armantomys*, *Microdyromys*, among others) have classically been inferred as inhabitants of open environments due to the simple morphology of their upper molars<sup>18</sup>. FC VI also includes terrestrial squirrels —also considered inhabitants of open landscapes— and cricetids<sup>22</sup>. In summary, FC V is made up of forest dwellers, whereas FC VI comprises open-environments adapted forms, which dominate in the southern province (Fig. 3).

Interestingly, although both faunal components present their highest values at the beginning of the interval analysed (Fig. 1), it appears that the peak of PCA factor 6 scores slightly preceded the one of PCA factor 5. This discrepancy might be related to the middle Miocene aridity peak on the Iberian Peninsula (around 9.5 Ma), which gradually diminished towards the Vallesian<sup>25,27,28</sup>. Nevertheless, the decline of Gliridae in terms of diversity, as well as the decrease in its relative abundance in rodent assemblages, becomes apparent during the latest middle Miocene, around 12 Ma<sup>29</sup>.

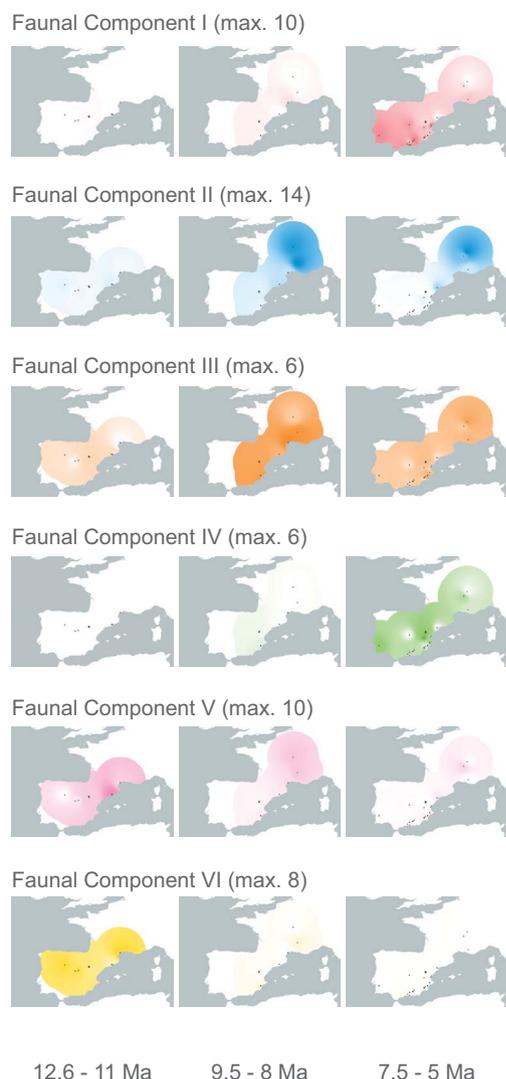
PCA factors 5 and 6 were negatively affected by global temperature cooling (negative correlation between PCA factor scores and  $\delta^{18}\text{O}$  values, see table 2). Despite their ecological differences, both faunal groups underwent a progressive demise concomitant with the cooling trend. Associated with this mid-Vallesian faunal change, formerly known as the Vallesian Crisis<sup>30,31</sup>, FC V and FC VI were succeeded by more open-habitats adapted faunas that characterised the following period.



**Figure 1** | Changes throughout time in the first six PCA factors in the two biogeographical provinces of the Iberocccitanian region. To visualize trends throughout the Miocene, we applied a local regression fitting (LOESS). The smoothing parameter  $\lambda$  controls the balance between the goodness-of-fit of the model (see method section). Different colours indicate each PCA factor.



**Figure 2** | Through-time variations in richness for the genera included in each Faunal Component. Results calculated for each fossil site in the northern and southern provinces of the Iberocctanian region are fitted with a local regression (LOESS). This kind of representation reduces the influence of extreme data, which makes it appropriate for trend interpretation. We chose the smoothness of the fitted LOESS ( $\lambda$ ) using generalised cross-validation (GCV) to avoid over fitting the observed data<sup>67</sup>. Colours indicate the correspondence with PCA factors in Fig. 1.



**Figure 3 | Species richness of FCs throughout time and space.** Species richness is plotted in three temporal windows. Color density proportional to the species richness in each locality. The higher colour density for each FC is set to its own richness maximum (in parentheses). Localities are represented by dark dots. We generated maps by using the interpolation tool implemented in QGIS with a distance interpolation parameter of 3. Our spatial interpolation was restricted to a radius of 500 km around each locality.

Earliest late Miocene faunal components. FC II and FC III constitute a second subset that includes genera presenting their highest richness values between approximately 11–7 Ma and decreasing drastically between 7 and 6 Ma (Fig. 2).

FC II includes sciurines—particularly flying squirrels—, dormice, hamsters and beavers, but also eomyids, zapodines, anomalomyids and one gerbil (Table 1). A total of 23 genera makes it the most diverse of all the Faunal Components. Several authors have recognised an ecological preference for forested habitats for most of the taxa in this set<sup>21,23,33–38</sup>. In fact, the genera grouped in this component are much more abundant in the northern province, reaching richness values of over ten species. Their richness was maintained until around 6 Ma (Fig. 2). Our results suggest that the northern province might have maintained the optimal humidity conditions in which the genera of FC II found propitious environments. This pattern is clearly exemplified by the flying squirrels, which were mainly restricted to the northern province and did not enter the southern province until the end of the Miocene<sup>40</sup>.

FC III included only seven genera, most of them Murine rodents (e.g. *Progonomys* or *Occitanomys*). The taxa included in this faunal component are among the most ubiquitous genera included in the present research, existing throughout the whole time lapse considered and recorded in most of the fossil sites of the Late Miocene (Fig. 3). This ubiquity likely stems from the fact that most of them have been described as inhabitants of open woodland areas<sup>12,41,42</sup>, an environment widely extended across a large portion of the Iberian Peninsula during the late Miocene<sup>26</sup>.

PCA factor 2 in the northern province was favoured by the global cooling trend (positive correlation between PCA factor scores and  $\delta^{18}\text{O}$  values, see table 2), suggesting that the global decrease in temperatures following the Middle Miocene favoured a group of forest-adapted northern faunas (Fig. 3). Nevertheless, a cooling trend, linked to an increase in aridity, occurred at the end of Miocene. As a result, the Northern Hemisphere underwent a climate deterioration associated with the expansion of open environments, and thus the diversity of forest-adapted forms declined, a fact that dramatically affected the flying squirrels of the studied area<sup>43</sup>.

Latest late Miocene faunal components. The end of the Miocene is characterised by the predominance of two different sets of muroids—mainly hamsters and mice—, included in FC I and FC IV (Fig. 2)<sup>21,32</sup>. FC I principally comprises genera of the subfamily Murinae, an important group in the Upper Miocene rodent faunas from Europe. Nonetheless, FC I is much more significant in the southern province than in the northern one (Fig. 3). Furthermore, this latest Miocene genera set included various rodent species with African and Asian affinities<sup>44–47</sup>, as well as a terrestrial squirrel, all of them associated with the development of arid environments<sup>48,49</sup>.

FC IV also grouped a set of forms classically associated with arid environments, including murines, microtoid cricetids, as well as porcupines and beavers with a preference for relatively dry habitats (Table 1)<sup>21,50–52</sup>. As previously seen for FC I, FC IV shows the expected geographic pattern for faunas with preferences for arid environments, with taxa limited to only a few fossil sites of the northern province (Fig. 3), whereas these taxa show higher species richness in the southern province through the late Miocene (Fig. 2 and Fig. 3).

We suggest that the prevalence of this arid-adapted forms (both FC I and FC IV) is related to the Messinian event<sup>19</sup>. The extent and impact of the Messinian Salinity event remain a matter of debate<sup>53–55</sup>. Nevertheless, our results suggest, however, a substitution of forest-adapted faunas by open-habitat related forms took place concomitant with the Messinian event. Our climatic analysis confirms this idea. PCA factors 1 and 4 in the southern province were favoured by the global cooling (positive correlation between PCA factor scores and  $\delta^{18}\text{O}$  values, see table 2) that gave rise to aridification of the ecosystems in central and southern Iberia<sup>26</sup>. In this case the groups favoured by the cooling trend in the south were associated with open environments, with opposite ecological preferences to the ones favoured by global cooling during the earliest late Miocene in the northern province (Fig. 3).

The combination of ecological and climatic analyses presented herein shed light on the ecological succession of rodent faunas that took place from the latest middle Miocene to the Miocene-Pliocene boundary. During this entire time interval, an almost continuous global cooling trend occurred<sup>24</sup> which was strongly associated with the ecological and evolutionary succession described. The first climate-driven event involved depletion of the faunal components V and VI associated with the end of the middle Miocene<sup>12</sup>. During the earliest late Miocene this cooling trend favoured the development of cool-adapted faunas (FC II) in the forested environments of the northern biogeographical province. Finally, during the latest Miocene, the global cooling rendered the inception of semiarid environments in the southern province, which harboured an increasing assemblage of aridity-adapted genera (FC I and FC IV)<sup>19,39,48</sup>.



**Table 2 | Results of the correlation analyses between the values of  $\delta^{18}\text{O}$  isotope<sup>24</sup> and the PCA factor scores for the fossil sites in each biogeographical province of the Iberocctanian region**

	Southern province		Northern province	
	r	p	r	p
Scores of PCA factor 1	0.409	<0.001	-0.279	0.159
Scores of PCA factor 2	0.197	0.062	0.534	0.004
Scores of PCA factor 3	0.201	0.058	0.310	0.116
Scores of PCA factor 4	0.375	<0.001	-0.109	0.590
Scores of PCA factor 5	-0.195	0.065	-0.571	0.002
Scores of PCA factor 6	-0.384	<0.001	-0.570	0.002

## Conclusions

The temporal variation of genera preponderance within Miocene rodent communities can be used to identify ecologically affine groups—faunal components—. Our macroecological fossil-based approach enables us to identify similarities in the temporal and spatial variations of these faunal components that link them to variations in global and regional climate. Identification of such patterns revealed the existence of differential responses within rodent faunas to a complex set of changing and interconnected circumstances, including variations in biogeography and environments over time.

## Methods

**Database.** The geographical range of the present research spans the Iberocctanian region (Iberian Peninsula and central–South eastern France; Fig. S4), comprising fossil localities from the latest Middle Miocene to the Miocene-Pliocene boundary (12.6 to 5.0 Ma; Supplementary information Fig. S4 and Table S3). This region is a remarkable area for the development of macroecological studies from a deep-time perspective due to the quantitative and qualitative importance of its fossil record<sup>49</sup>. Interestingly, in relation to the rest of Europe, the study area exhibits environmental differences which persist in time due to its isolated position in the westernmost part of Europe<sup>51,56,57</sup>, which characterised this region as an ecological refuge during particular time lapses<sup>19,20,58</sup>.

Additionally, in this region two environmentally distinctive mammalian bioprovinces arise<sup>20,59</sup>, recognizable since the Eocene<sup>60,61</sup>. The northern province includes fossil sites from the Rhône, Provence, Cuceron-Basse Durance and Languedoc-Rousillon basins from South-Eastern France, and the Vallès-Penedès basin from Catalonia (North eastern Spain). All the other fossil sites from the Iberian Peninsula are included in the southern province and are located at Alfambra-Teruel, Alicante, Baixo Tejo, Castellón, Calatayud-Daroca, Duero, Fortuna, Granada, Guadix-Baza, Híjar, Murcia, Tajo, and Valencia basins (See supplementary information Table S3).

We compiled a database of rodent species recorded at each fossil site included in this study. The species list per fossil site was based upon a reviewed compilation from the literature and updated to the latest taxonomy<sup>20</sup>. Additionally, the minimum sample required to include a fossil site in the present study was 100 molars (including first and second upper and lower molars). This number is considered to be the minimum necessary to render a representative sample of the original assemblage<sup>62</sup>. This restriction was overlooked in the case of poor localities characterised by their interesting geographic location or stratigraphical importance.

We employed this dataset of rodent species to compile a matrix with information on the percentage of species of each genus in each fossil site. Finally, our database considers 973 records of 67 rodent genera in 117 Iberocctanian fossil sites (See supplementary information Table S1). We used species percentages (relative richness) rather than number of species to avoid the potential influence of species richness on the results<sup>63</sup>, which can be affected by sampling biases<sup>64</sup>.

**Identification of faunal components.** By applying Principal Component Analyses (PCA) to a sites/genera percentage matrix, we classified rodent genera into groups with comparable patterns in the variation of species richness in time and space, which we call faunal components. The PCA enabled us to portray the changes in the taxonomic structure of these Iberocctanian rodent faunas<sup>12,63,65</sup> by reducing the number of original variables (67 genera) to a series of linear combinations among them (PCA factors). To maximize the sum of the within-factor variances, we used a VARIMAX rotated PCA model. The aim of this additional rotation was to obtain a simple structure where the coefficients within a factor are as close to one or zero as possible<sup>66</sup>.

In order to establish the faunal components, we selected for each one the genera that provide their highest contribution to a given PCA factor. That is, each genus belongs to only one faunal component based on which PCA factor includes the highest value for this genus in the escalated components matrix. Subsequently, we explored the species richness (number of species of each genera) for the genera comprised in each faunal component for each province. We did so because raw

diversity patterns can provide complementary and insightful information for the interpretation of the changes in community structure.

We plotted the PCA factor scores and faunal components richness of each fossil site against time and applied a local regression fitting (LOESS) over the data to visualize their trend throughout time. This kind of representation reduces the influence of extreme data, which makes it appropriate for trend interpretation.

The number of sites in the two provinces considered differs: 90 sites in 13 basins in the southern province, 27 sites in 5 basins in the northern province. To assess how this difference might affect our results, we performed a complementary analysis following a bootstrapping approach. The sites per basin ratios are 5.4 and 6.9 in the northern and southern provinces respectively. To equal the sampling effort in both provinces, only 70 sites should be sampled in the southern province. Thus, we bootstrapped 1000 times 70 of the 90 sites without replacement, and fitted 1000 species-diversity through-time curves for each of the FC. We then condensed these curves while plotting the confidence interval of the fitted values (see electronic supplementary information Figure S2). The patterns recovered from the bootstrapped subsets are highly consistent with those obtained from the raw data.

The geographical patterns of the species richness of each FC were analysed with the use of QGIS (<http://www.qgis.org/en/site/>). The interpolation tool implemented in QGIS was set with a distance interpolation parameter of 3. Our spatial interpolation was restricted to a radius of 500 km around each locality. We mapped these patterns in three temporal windows (12–6 to 11, 9.5 to 8 and 7.5 to 5 Ma), which were selected to represent the critical peaks and troughs of FC richness.

Finally, we evaluated the potential relationship between global climate changes and the temporal trends in rodent community structure by testing the correlation between the PCA factor scores of the fossil sites and the oxygen isotopic value ( $\delta^{18}\text{O}$ ) associated with each locality as a proxy of the palaeotemperature. In order to perform this analysis, we fitted a smoothed curve to the isotopic information<sup>24</sup> and interpolated an isotopic value for the age of each fossil site. Due to environmental differences between the northern and southern biogeographic provinces, independent correlations were calculated for the two bioprovinces.

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## Author contributions

A.R.C.G., J.L.C. and M.H.F. conceptualized the research; A.R.C.G. prepared and analysed data; J.L.C. made Bootstrap and QGIS analysis; and A.R.C.G., J.L.C., M.H.F. and M.A.S. wrote the paper. All authors contributed to the interpretation of the data and provided significant input to the final manuscript.



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