

10 Evaluating the roles of connectivity and environment on faunal turnover: patterns in recent and fossil Iberian mammals

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10.1 Abstract

The role of dispersal events in shaping patterns of geographic differentiation of biotas has been often studied regarding to invasive events occurring in short periods of time. However, migrations of species from one area to another are occurring continuously. Thus, patterns on differentiation diversity may be affected by the connectivity among areas. We provide evidence of this fact using the recent mammal faunas at the Iberian Peninsula. When compared with differences in environment and habitat structure, connectivity-mediated distances were the most important factor affecting β -diversity patterns at 100x100 km scale. Moreover, most of the explanatory capacity of environmental differences could not be separated from that attributable to connectivity. We developed a model that links patterns in β -diversity with geomorphologically-based connectivity using these recent data, and tested it on the patterns of macromammal variation among sedimentary basins during the Iberian Neogene. β -diversity values were much higher than those observed for recent faunas, and our model was unable to predict Neogene patterns. A critical discussion on the causes of this lack of agreement among recent patterns and those observed from fossil data is provided.

Keywords: geographic connectivity, Iberian mammals, geomorphology, Neogene and recent faunas, beta diversity, faunistic similarity, environmental differences.

10.2 Introduction

Most times, biological invasions are regarded as discrete events in time. In a few years, or decades, single species or complete faunas are able to colonize broad territories, competing with, and even displacing, native species and communities (see some examples at, e.g., Vitousek et al. 1987, Niemela and Spence 1991, and reviews at Hengeveld 1989, Shigesada and Kawasaki 1997, Levine and D'Antonio 1999, or Sakai et al. 2001). Most of these invasions are continuously taking place in a silent and gradual way. As Kozłowski (1999) states, species produce numerous offspring, which migrate in a density-dependent regulatory mechanism. Thus, the world is flooded with migrants of different species, which can suffer microevolutionary changes in the newly-established populations (e.g. Hendry and Kinnison 2001). This mixture of dispersal and local microevolutionary processes is one of the causes of biodiversity, assuring the immense, permanent variability of nature, and regulating the genetic and ecological structure of populations via permanent gene flow in heterogeneous landscapes (Kozłowski, 1999), as well as the structure of local and regional communities (see, e.g., Cornell and Lawton 1992).

Although implicitly accepted as a necessary part of the faunistic differences among different areas, the importance of these 'shadow invasions' in shaping the variation in community composition remains frequently unnoticed. Other factors, such as environmental variability or differences in habitat structure have been claimed to play significant roles in the structure of ecological communities. However, recent works have found significant relationships between spatial distance among local communities, and community dissimilarity (e.g. Duivenvoorden et al. 2002). These differences could be attributed to increasing differences in environmental conditions between increasingly distant sites due to environmental gradients (see, e.g., Pereira and Pires da Fonseca 2003). However, spatial distance and, most accurately, connectivity among areas, together with dispersal ability, mediates the success of species in reaching a new locality. Here, connectivity is defined as the facility of movement

between two areas, taking into account geomorphologic and/or landscape characteristics.

In this framework, differences in the connectivity among areas could give rise to differences in community composition. To carry out a preliminary test of this hypothesis at a regional scale, in the first part of this work we use data on the community composition of recent Iberian mammals to evaluate the relative importance of differences in connectivity, environment (climate and geology) and habitat over differentiation diversity, measured as β -diversity.

Most times, the relationships of the above mentioned factors (environment and/or habitat) with the ecological responses of several recent mammal species have been used to extrapolate past conditions from fossil faunas, a point that we have criticized extensively (Rodríguez 1999, Rodríguez and Nieto 2003, Hortal et al. in revision; see discussion). However, to test if the present relationship between connectivity among areas and β -diversity could be extrapolated to the past, we have developed a function relating both variables using recent data. Then, we have tested the performance of our model on the mammal fossil record of the Iberian Neogene. Finally, we assess the possible effects of well known invasive and/or macroevolutionary events over the β -diversity patterns throughout this age.

10.3 Assessing the role of environment, habitat and connectivity on recent mammal communities

As we commented before, we carry out a preliminary test on how the differences among areas in i) environment and ii) habitat structure, and iii) connectivity, shape the patterns of faunistic differentiation of recent Iberian mammals. To avoid effects of area size and/or data coverage, we have used the cells from the UTM 100x100 km grid where more than 90% of their total area is occupied by land surface at the Iberian Peninsula. Grid cell size was selected to approximate to the area of the sedimentary basins that we use as units of analysis for the fossil data. 52 Iberian 100x100 km resolution grid squares fulfilled these criteria, so we use them to develop three distance matrices for the abovementioned three factors (see Figure 1). The methodological limitations of the GIS and the community analysis package used, prevented us from developing the high number of possible pairwise comparisons among these grid squares (1300). Thus, we compare the distance values for 50 pairs of squares selected at random with the β -

diversity scores obtained from the pairwise comparisons of the mammal faunas of these squares.

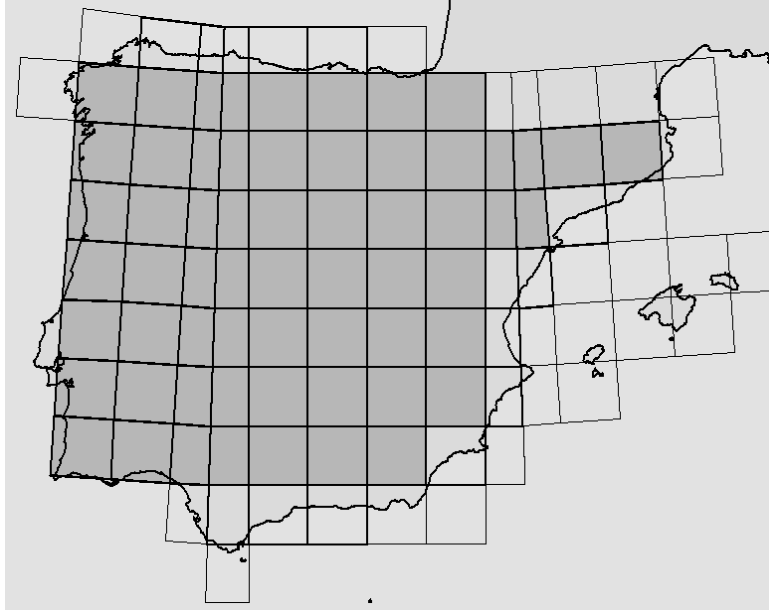


Fig. 1. Spatial location of the 52 squares (dark grey) from the UTM 100 km grid used for the recent fauna analyses (see text)

10.3.1 Estimation of present environmental and habitat differences between areas

To assess the influence of variation in environmental conditions and habitat structure on recent mammal communities, we developed two matrices of distances among the UTM 100x100 grid squares:

*The first one, d_{env} , accounts for environmental variation. It was built using the information from six climatic variables (minimum, maximum and mean annual temperature, mean annual and summer precipitation, and percentage of sunny hours per year), and three bedrock geologic (calcareous rock, acid rock and clay area). Climate data extracted from the 50x50 km resolution data provided by W. Cramer (CLIMATE database version 2; <http://www.pik-potsdam.de/~cramer/climate.html>). To obtain bedrock data, we used a previously digitised three-category map (IGN 1995). All these variables were successfully used in other analyses on the distribution of species richness and composition of several groups of

Iberian plants and insects (e.g., Lobo et al. 2001, Lobo and Martín-Piera 2002, or Hortal et al. 2004). These analyses usually include geomorphologic and structural variables, such as altitudes, slopes, aspects, etc. However, we use such information to develop friction surfaces and connectivity analyses (see below). Thus, we have excluded them from the calculation of the environmental matrix, in order to avoid self-replication and to separate more clearly both sources of faunistic variability.

*The second one, d_{luc} , accounts for the differences in the land use/land cover of each area, that is, for differences in habitat structure among areas. To develop this matrix, the original CORINE Land Use/Land Cover map (EEA 2000) were reclassified into 13 categories (urban areas, dry cultures, irrigated cultures, patchy cultures, olive, vineyard and fruit plantations, anthropogenic pastures, natural pastures, broadleaf forests, conifer forests, mixed forests, shrubland, bare rock and land masses). The percentage of land coverage devoted to each category was extracted using GIS techniques. Similar variables were also successfully used in several of the formerly related studies.

Following the recommendations of Legendre and Legendre (1998), after the standardization of the truly continuous variables (those related to climate), we used the Gower Similarity Index (Gower 1971) to measure the environmental and habitat proximities among grid squares. In the case of the development of the d_{env} matrix, different weights were assigned to bedrock and climate variables, to account for the differential importance of each group of environmental variables in the distribution of the species (see discussion at Hortal and Lobo 2005). Although bedrock geology is not a direct determinant of variations in mammal communities, it does for plants (see, e.g., Lobo et al. 2001 for the Iberian Peninsula), a well known determinant of mammal diversity (see, e.g., Olf et al. 2002 or Cristoffer and Peres 2003). Thus, substrate composition may have an indirect effect over mammal communities. Although no analysis is available on the different weights of geology and climate in the configuration of mammal communities (see Hortal and Lobo 2005 for an example of such analysis on Iberian dung beetles), we have assumed the latter having greater importance. In absence of any hypotheses of the magnitude of such difference, and following the empirical evidence obtained by Hortal and Lobo (2005), climate was assumed to be three times more important than geology. Thus, every climatic variable had a weight of 1/2 (3/6 variables), giving a total weight of 3 to climate (0.5 x 6 climatic variables). In the same way, every geologic category had a weight of 1/3 (1/3 variables), and geology a total weight of 1 (0.33 x 3 variables). The resulting similarity matrices (calculations made with Clustan Graphics software; Clustan Ltd.

2002) were transformed into distance matrices by calculating the inverse of the index value (that is, $d = 1 - \text{Gower value}$).

10.3.2 Estimation of connectivity between areas

Both habitat structure and topography play a well known role in the connectivity among areas. Our main objective is to analyze the relationship between connectivity and β -diversity in both present times and during the Neogene. Since we lack accurate data to estimate connectivity during the Neogene, we will use recent data to extrapolate past conditions in order to estimate past connectivity. We assume that environmental conditions strongly varied during the Neogene, so we have chosen geomorphology as the factor that remained more constant during this period.

In spite of the differential effects on climate changes throughout the Iberian Peninsula (see, e.g., maps in Adams 1998), the spatial location of the main geographic accidents (mountain chains, plateaus, valleys, etc.) has not suffered dramatic changes. It is true that topographic variations due to the Alpine Orogeny, and sea level variations due to glaciation processes, have led to great temporal differences in the spatial configuration of habitats in the Iberian Peninsula. However, most current valleys, plateaus and mountain chains have been valleys (or sea intrusions) plateaus and mountain chains for a long period of time. Thus, it can be assumed that, if point A is best connected to point B than to point C in the present, it remained so throughout the last MYs. Thus, we have assumed as a working hypothesis, that their effect on broad scale differences in mammal communities could have remained constant. This assumption should not be hold for true, as we are going to see below.

The spatial configuration of the physical matrix where dispersal occurs, limits or facilitates the migrations of species (see, e.g., Lobo and Halfpeter 2000, or Spector 2002), thus determining the connectivity among areas. For example, the direction of frictional effects to movement (that is, factors that increase the cost of moving through a territory) is important in mountain environments. The direction of slopes affects the efforts needed to cross an area depending upon the direction of movement (i.e., up, down, or along a slope). Areas with the same slope values, but at different directions (aspect), might have very different frictions for the dispersal in a given direction. On the one hand, longitudinal mountains (that is, those having an east-west configuration) can act as barriers to latitudinal (north-south) dispersal. The harsh conditions appearing at high altitudes impede the communication between both sides (see, e.g. Brown and Lomolino 1998, or Bhattarai and Vetaas 2003), thus diminishing the relationship

between northwards and southwards faunas. On the other, latitudinal mountain chains (those placed in a north-to-south direction), in spite of being barriers for the longitudinal (east-west) dispersal, can also act as corridors for latitudinal movements. The climatic gradients they produce may permit to the populations or individuals of a given species to reach suitable conditions just by rapid shifts in altitude. Thus, latitudinal mountain chains facilitate latitudinal movements by providing corridors of suitable habitat conditions, allowing communication between faunas of sites located at different latitudes.

We have taken this issue into account to calculate the distances between areas, by means of a connectivity analysis in a GIS environment. 1 km² resolution altitude data was obtained from a global Digital Elevation Model (Clark Labs 2000). Aspect and slope maps were derived from this DEM using Idrisi software (Clark Labs 2001). Then, we developed connectivity distance images, where the friction-mediated cost of moving to each spatial object studied (in this case, 100x100 km squares) from each 1 km² pixel is stored. In the case of recent data, these cost distances are calculated from the centroids of each 100x100 km square. In the case of the fossil faunas, several centroids were located at each basin, and the cost distances to each pixel were calculated from the nearest one. Anisotropic cost algorithms implemented in Idrisi GIS software calculate such connectivity distance images from three different maps (see Clark Labs 2001):

*A magnitude of friction surface, where different slope values are reclassified into friction values. A sigmoid-shape relationship between slope and friction was assumed, with low increments of cost of movement at low slope values, and progressively higher increments. Friction was assumed to be minimum at 0°, and maximum at slopes of 50° or higher.

*A map of the direction of friction (anisotropic costs; see Clark Labs 2001). A new GIS coverage was obtained from the aspect map, where longitudinal aspects were assigned to frictions in latitudinal directions, and latitudinal aspects did to longitudinal directions. This image is used to weight the cost of movement through each pixel. Thus, movements are restricted by transversal mountains, under the assumption that mountain chains act as barriers to the movement of most species. This may be especially true during cold periods, where the extreme conditions happening at high altitudes may difficult migrations of many of the temperate, mediterranean and semi-tropical species present in the Iberian Peninsula.

*An isotropic friction surface, representing the non-directional frictions to the movement. In this case, we used just altitude, as it constitutes a proxy for the environmental variability that may be similar effects through time.

In this case, a sigmoid-shape relationship was also assumed, taking current altitudes of 1000 m.a.s.l. as completely suitable to movements, and those higher to 5000 (non-existent in the Iberian Peninsula) to be completely unsuitable. These values were selected to provide a realistic simulation of the effects of altitude on dispersal; many mammal species can disperse easily up to an intermediate altitude, and the difficulty of movement increases exponentially from these point, up to a ceiling sited at extreme altitudes, where environmental conditions do not permit the survival of migrants. This way, moving through high altitude mountains is possible, but at high costs.

Using these three cost images, a connectivity distance image is calculated for each 100x100 km grid cell (or sedimentary basin, see below). Then, the distance of connectivity (d_{con}) from each cell to another is calculated using a least-cost pathway algorithm (see Clark Labs 2001). This analysis calculates the shortest way from a given point to another using the connectivity distance image of one of them, developing a pathway that minimizes the costs of moving through the friction surface. The spatial location of the 50 pathways developed for recent faunas is shown in Figure 2 (see another example in Figure 6 below). d_{con} values were calculated as the sum of the costs of moving through 1 km² each pixel in the pathway. The higher the value of d_{con} , the higher the difficulty to move from a point to the other. This way, we produced a triangular distance matrix among grid cells.

10.3.3 β -diversity estimation

Recent mammal community data comes from the current atlas of the distribution of Spanish terrestrial mammals (Palomo and Gisbert 2002). We have extracted checklists from the previously defined grid cells. To measure differences in composition from such presence/absence data, we have chosen β_w , the classic measure from Whittaker (1960). Although a few newly-developed estimators present better properties (e.g., additivity or usability with nested areas; see Koleff et al. 2003), this measure has been extensively used in the literature, and has the crucial properties of symmetry and independence of sample size (see Wilson and Shmida 1984, Magurran 1988, and Koleff et al. 2003). This index relates the total number of species recorded in the two areas being compared (in this case, grid squares), with the average number of species found within them. According to the formulation of Koleff et al. (2003), this index is calculated as:

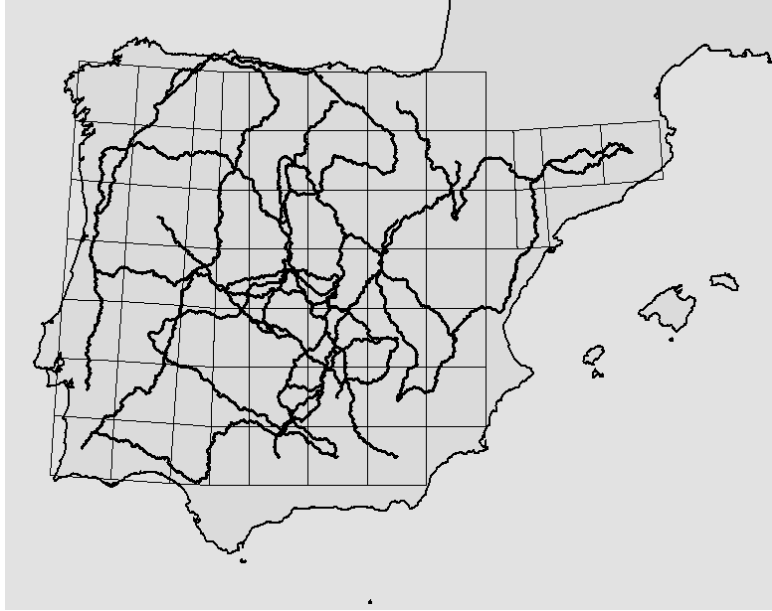


Fig. 2. Pathways obtained in the recent fauna connectivity analyses. Each line shows the spatial location of the least-cost pathway between the centroids of one of the pairs of grid cells analyzed (thin squares), using a geomorphologically-based friction surface (see text)

$$\beta_w = \frac{a + b + c}{(2a + b + c)/2} - 1 \quad (10.1)$$

where a is the number of species found in both samples, b is the number of species found in the first grid cell but not in the second, and c is the number of species found in the second grid cell but not in the first one. As mentioned before, we used the 50 pairs of 100x100 km grid squares selected at random, and calculated β_w scores using Species Diversity and Richness 3.0 software (Henderson and Seaby 2002). These species replacement scores were mainly low, ranging from 0.0423 to 0.3628, with a mean β_w value of 0.2037 (± 0.0805 SD). Interestingly, the resulting values showed a clear relationship with d_{con} scores (Figure 3; see also Table 2 below).

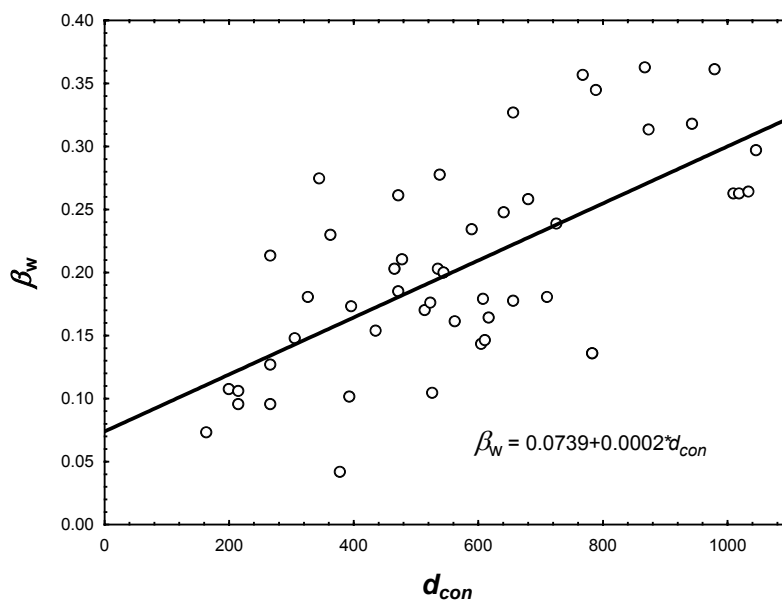


Fig. 3. Relationship between mammal differentiation diversity (β_w ; see text) and connectivity-mediated distance (d_{con}). Circles correspond to the 50 pairwise comparisons between pairs of 100x100 km UTM cells, and the line and function correspond to the linear model developed using common regression techniques (see text)

10.3.4 Determinants of β -diversity

Once the distance matrices accounting for differences in environment, habitat and connectivity are developed, we have carried out a preliminary analysis of their relative importance in shaping the variation in mammal faunistic composition between pairs of areas, using the 50 previously defined pairwise comparisons.

After standardizing these variables, and assessing their normality, their single importance was calculated by means of the regression techniques included in the General Regression Models (GRM; see, e.g., Dobson 1999, or StatSoft 2001). Adjusted R^2 statistic has been used to estimate the amount of variance explained by each factor (see Table 1), applying the correction for negative Adjusted R^2 values suggested by Legendre and Legendre (1998). Interestingly, whilst the effect of environmental distances was small (around 10%), and differences in habitat were non-

significant, connectivity between pairs of areas explained 45.9% of their β_w scores. A full model, based on the three kinds of distances, explained up to 47.1% of total variance.

Table 1. Results from the General Regression Models (that is, ANOVA results; see StatSoft 2001) using environmental, habitat structure, and connectivity distances over β_w . *df* is the number of degrees of freedom of the model; *F* is the Snedecor's *F* statistic; *Mult. R*, *Mult. R²*, and *Adj. R²* are the multiple and adjusted estimates the amount of variance explained by each model. *Adj. R²* scores were corrected for negative values according to the method suggested by Legendre and Legendre (1998). Predictor names as in text. ** is $p < 0.01$, * is $p < 0.05$, and n.s. is non significant

| Predictor | Df | F | Mult. R | Mult. R ² | Adj. R ² |
|--------------------------------|----|---------------|---------|----------------------|---------------------|
| Full regression models | | | | | |
| d_{env} | 48 | 5.366* | 0.317 | 0.101 | 0.100 |
| d_{lulc} | 48 | 2.041 n.s. | 0.202 | 0.041 | 0.039 |
| d_{con} | 48 | 39.621** | 0.672 | 0.452 | 0.459 |
| $d_{env} + d_{lulc}$ | 47 | 2.817 n.s. | 0.327 | 0.107 | 0.087 |
| $d_{env} + d_{con}$ | 47 | 22.050** | 0.696 | 0.484 | 0.481 |
| $d_{lulc} + d_{con}$ | 47 | 20.444** | 0.682 | 0.465 | 0.461 |
| $d_{env} + d_{lulc} + d_{con}$ | 46 | 14.524** | 0.697 | 0.486 | 0.471 |
| Partial regression models | | | | | |
| rd_{env} | 48 | 1.041 n.s. | 0.146 | 0.021 | 0.019 |
| rd_{lulc} | 48 | 0.113 n.s. | 0.049 | 0.002 | 0.000 |
| rd_{con} | 48 | 29.344** | 0.616 | 0.379 | 0.385 |

To partition the effects of these factors into their independent and joint components (e.g., the amount of β_w variation that can be attributed to the single effect of d_{con} , independently from the variations in d_{env} or d_{lulc} , or the amount of variation that is due to the joint effect of d_{con} and d_{env}), we used partial regression analyses (see Legendre and Legendre 1998, or Lichstein et al. 2002). In these analyses, each predictor (or group of predictors) is regressed against all the others. The resulting residuals are retained, thus representing the variability in each predictor that is independent from the others. This way, we used GRM analyses to extract three new variables:

rd_{env} (the residuals of regressing d_{env} over d_{lulc} and d_{con}), rd_{lulc} (from d_{lulc} over d_{env} and d_{con}), and rd_{con} (from d_{con} over d_{env} and d_{lulc}). We then regressed β_w values over these new variables, thus obtaining the independent effects of the three factors (see Table 1). Here, it is remarkable that the effect of the environmental differences falls out of significance, as most of its explanatory capability can not be separated from that of the connectivity.

Table 2. Significance and parameter estimation of the model relating the scores of β_w between UTM 100x100 grid squares and connectivity distances ($\beta_w = \text{Intercept} + \text{estimate} * d_{con}$; see also Figure 3), developed from the data of the 50 pairwise comparisons of recent Iberian mammals. Estimate shows the parameter scores in the model, *Std. Err.* does for the standard error of these estimates, *t* for the *t* statistic, and *cl-95%* and *cl+95%* are the lower and upper confidence limits for the estimates. The rest of the abbreviations as in text and Table 1

| | <i>df</i> | F | Mult. <i>R</i> | Mult. <i>R</i> ² | Adj. <i>R</i> ² |
|-----------------------------|-----------|------------------|----------------|-----------------------------|----------------------------|
| <u>Model significance</u> | 48 | 39.621** | 0.672 | 0.452 | 0.441 |
| <u>Parameter estimation</u> | Estimate | <i>Std. Err.</i> | <i>t</i> | <i>cl-95%</i> | <i>cl+95%</i> |
| Intercept | 0.073893 | 0.022305 | 3.312** | 0.029045 | 0.118743 |
| d_{con} | 0.000226 | 0.000036 | 6.295** | 0.000154 | 0.000298 |

We used the equation system proposed by Borcard et al. (1992) to fully partition the variation in β_w due to these three effects into nine components describing their independent and joint influences (see examples in Lobo et al. 2001, 2004, or Pereira and Pires da Fonseca 2003). The effect of pure connectivity appears as being almost the unique single effect in shaping faunistic differences (Figure 4). This analysis also reveals that the effect of environmental distances cannot be separated from that of the connectivity. The high amount of unexplained variance (more than 50%) puts into evidence that the here considered factors may not be the only ones affecting β_w patterns. Other effects, such as historical contingent events, or other environmental effects not included in our analysis, may underlie this pattern. Here, it is important to take into account that the spatial scale used (grain size) may not be the best to cover the effects of differences in landscape structure (usually studied at 1x1 and 10x10 km grain sizes) and environment (mostly studied at 10x10 and 50x50 km grain sizes) (see discussions at Whittaker et al. 2001, Willis and Whittaker 2002, and Blackburn and Gaston 2002). Moreover, the weight assignation to the different factors in the construction of the d_{env} matrix was arbitrary, and no

assessment is available on its accuracy to describe the environmental differences important for mammal diversity.

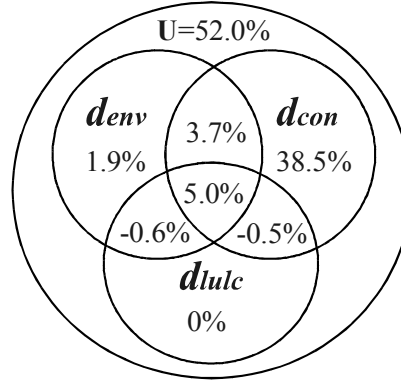


Fig. 4. Variation in β_w linked to the three variation factors studied (abbreviations following text). U is the unexplained variation. Explained variation values correspond to Adjusted R^2 values, corrected for negative values. The negative values of the joint variation of d_{ulc} and d_{env} , and d_{ulc} and d_{con} , may be due to synergic effects, but must be taken with caution due to the low explanatory value of this factor

In spite of these considerations, however being partial and preliminary, our analyses show a great effect of connectivity between pairs of areas in the replacement of faunas. Thus, we have used the original d_{con} data to develop a model that relates connectivity and β_w (see Table 2 and Figure 3).

Table 3. Significance and parameter estimation of the model relating the scores of β_w between UTM 100x100 grid squares and connectivity distances ($\beta_w = \text{Intercept} + \text{estimate} * d_{con}$; see also Figure 3), developed from the data of the 50 pairwise comparisons of recent Iberian mammals. Estimate shows the parameter scores in the model, *Std. Err.* does for the standard error of these estimates, *t* for the *t* statistic, and *cl-95%* and *cl+95%* are the lower and upper confidence limits for the estimates. The rest of the abbreviations as in text and Table 1

| | <i>df</i> | F | Mult. <i>R</i> | Mult. R^2 | Adj. R^2 |
|-----------------------------|-----------|------------------|----------------|---------------|---------------|
| <u>Model significance</u> | 48 | 39.621** | 0.672 | 0.452 | 0.441 |
| <u>Parameter estimation</u> | Estimate | <i>Std. Err.</i> | <i>t</i> | <i>cl-95%</i> | <i>cl+95%</i> |
| Intercept | 0.073893 | 0.022305 | 3.312** | 0.029045 | 0.118743 |
| d_{con} | 0.000226 | 0.000036 | 6.295** | 0.000154 | 0.000298 |

10.4 Assessing connectivity, model performance, and β -diversity patterns in the Iberian mammals during the Neogene

In this section, we test if our model on recent mammals could be used to assess the relationship between connectivity and faunistic replacement between regions in the Iberian Neogene. Therefore, we try to characterize β -diversity patterns through this period from the data provided by well known sites, to identify possible episodes of isolation between regional faunas and/or massive migrations.

10.4.1 Could β -diversity patterns be extrapolated to the past using connectivity between areas?

Neogene (23 to 2 Ma) mammal record is extraordinarily rich in Spain where more than 200 fossil sites have been already unearthed. The data used in the present analysis come from an updated compilation of the regional taxonomic diversity recorded in Spain published by Nieto et al. (2003). Only macromammal species are considered, excluding Chiroptera, Rodentia, and Insectivora, despite the relevant information that microammals may provide. Differences in the sampling methodology and effort as well as the fact that in most cases both records come from different localities, make difficult to join both data. Species is used as taxonomical unit for the present analysis since Spanish mammals have been intensively studied and their taxonomy is well established (see Nieto et al. 2003 for further discussion and references). Using a more stable taxonomic category, like genus, will reduce the diversity information providing only a minor increase in taxonomical stability. For our analyses, the regional diversity was estimated using basins as spatial units (see figure 5), and Mein's MN zones (Mein 1975) as temporal units. This zonation, based on the mammalian faunal composition, is the most commonly used temporal scale for the Neogene continental record of Europe.

We have obtained regional faunas by aggregating the species present in all the sites of the sedimentary basin during each biozone. To avoid extreme sampling biases, we have used for the analyses only those basins with data for 3 or more sites in the biozone. Then, we calculated β_w scores for all the possible pairwise comparisons of areas. All these scores, ranging from 0.4118 to 0.9333 (mean value = 0.7239 ± 0.1347), were much higher than the maximum β_w observed with recent faunas (see Table 3). The use

of macromammals for the analysis, instead of using all mammals, should not account for such a pattern, as they are known to have broader distribution ranges (e.g. Blackburn and Gaston 1996), thus producing smaller expected β_w values. To test the influence of possible biases in the fossil record of the basins studied on this result, we have computed Spearman Rank correlation tests for the relationship of β_w and several variables used as proxies for the completeness of the record. These variables are the total number of species in the two basins compared (N_{sp}), their variance (Var_{sp}) and the number of sites per biozone (N_s). β_w is not significantly correlated to any one of the variables considered. This result suggests that the described pattern of high species replacement between basins can not be fully attributed to the incompleteness of the fossil record.



Fig. 5. Spatial location of the sedimentary basins used to group the Neogene deposits into different mammal faunistic regions. (Eb) Ebro; (Tj) Tajo; (Dr) Duero; (CT) Calatayud-Teruel; (VP) Vallés-Penedés; (Lv) Levantine basins; (Bt) Betic basins.

Table 4. Spearman rank-correlation test for the relationship among β_w and three variables used as proxies for fossil record completeness. N_{sp} = number of species in each pair of basins used for comparison; $Var_{N_{sp}}$ = variance in the number of species of these two basins; N_s = number of sites in the biozone

| | N | Spearman | t(N-2) | p-level |
|--------------------------|----|----------|--------|---------|
| β_w / N_{sp} | 19 | -0.326 | 1.421 | 0.173 |
| β_w / N_s | 19 | 0.214 | 0.901 | 0.380 |
| $\beta_w / Var_{N_{sp}}$ | 19 | 0.276 | 1.185 | 0.252 |

Connectivity between sedimentary basins was assessed by calculating minimum cost pathways using the same technique and cost maps formerly described. Here underlies the assumption that geomorphology-mediated connectivity among areas has remained constant enough during the last 23 Myr in the Iberian Peninsula. It is well known that many geological changes have happened in the last 23 million years in the Iberian Peninsula, including four important orogenic events (Pickford & Morales 1994). The main effect of these geological and climatic changes has been a gradual transformation from the former endorheic basins to present exorheic ones. However, its main structural configuration, that is, the positions of large mountain chains and basins has remained constant, so the basins recognized in the Neogene can still be recognized today (except the Baetic mountain chain and Guadalquivir basin, appeared during the Neogene; see Rögl 1999). To what extent such similarities in the connectivity among areas are enough for the present analysis are indirectly tested by our results.

For each basin, one or more centroids were assessed using the ‘center of mass’ technique (that is, one or more subpolygons were identified for each basin, and the mean of the latitude and longitude of all their perimeter points was used as its centroid; see details in Bosque Sendra 1997). Then, connectivity pathways between each pair of basins were calculated between the two nearest centroids in the friction surface. The results of this analysis could aid to identify possible migration corridors (that is, areas of heavy transit of species) in the Iberian Peninsula (see Figure 6), because the lines that connect basins suggest the location of the pathway that minimizes the cost of migrations.

We have used our model ($\beta_w = 0.073896 + 0.000226 \cdot d_{con}$; see Table 2 and Figure 3) to predict the species replacement scores between these pairs of basins (see results in Table 4). As could be expected, given the great differences between the value observed at recent and Neogene faunas, the model was not able to predict correctly any β_w score, being predicted and observed scores not related (Spearman $r = -0.2957$; $N = 19$; $t_{(N-2)} = -1.2761$; $p = 0.2190$).

Thus, the preliminary assumption of the maintenance through time of the relationship between β_w -diversity and geomorphologic connectivity is not supported by our analyses. However, it is important to take into account that, in this case, lack of evidence could not be due to lack of pattern.

The basic assumption of this analysis is that geomorphology-mediated connectivity among areas has remained constant enough during the last 20 Myr in the Iberian Peninsula.

Table 5. Comparisons among mammal Neogene regional faunas. Biozones are the Mammal Neogene biotic periods, following Mein (1975; see text). Basins are the sedimentary basins of each period, following codes as in Figure 5). β_w Obs. and β_w Prd. are, respectively, the observed species replacement scores, and the scores predicted by the model developed from recent data (see Table 2 and Figure 3). Resid. are the residuals from this model, *Std. Err.* the standard error for each β_w estimate, and *cl -95%* and *cl +95%* are its confidence limits

| Biozone | Basins | d_{con} | β_w Obs. | β_w Prd. | Resid. | Std. Err. | Cl -95% | cl +95% |
|---------|--------|-----------|----------------|----------------|--------|-----------|---------|---------|
| MN2 | Tj-Dr | 415.5 | 0.8519 | 0.1679 | 0.6840 | 0.0102 | 0.1473 | 0.1884 |
| MN3 | CT-VP | 503.5 | 0.5385 | 0.1878 | 0.3507 | 0.0089 | 0.1699 | 0.2056 |
| MN4 | Tj-CT | 426.8 | 0.9000 | 0.1704 | 0.7296 | 0.0100 | 0.1503 | 0.1906 |
| | Tj-VP | 757.0 | 0.6000 | 0.2451 | 0.3549 | 0.0108 | 0.2235 | 0.2667 |
| | CT-VP | 503.5 | 0.7619 | 0.1878 | 0.5741 | 0.0089 | 0.1699 | 0.2056 |
| MN5 | Tj-CT | 426.8 | 0.7500 | 0.1704 | 0.5796 | 0.0100 | 0.1503 | 0.1906 |
| MN6 | Tj-CT | 426.8 | 0.4118 | 0.1704 | 0.2414 | 0.0100 | 0.1503 | 0.1906 |
| MN7/8 | Dr-CT | 692.4 | 0.6279 | 0.2305 | 0.3974 | 0.0095 | 0.2114 | 0.2496 |
| | Dr-VP | 1050.8 | 0.6800 | 0.3116 | 0.3684 | 0.0191 | 0.2731 | 0.3500 |
| | CT-VP | 503.5 | 0.6471 | 0.1878 | 0.4593 | 0.0089 | 0.1699 | 0.2056 |
| MN9 | Dr-CT | 692.4 | 0.7447 | 0.2305 | 0.5142 | 0.0095 | 0.2114 | 0.2496 |
| | Dr-VP | 1050.8 | 0.6444 | 0.3116 | 0.3328 | 0.0191 | 0.2731 | 0.3500 |
| | CT-VP | 503.5 | 0.7108 | 0.1878 | 0.5230 | 0.0089 | 0.1699 | 0.2056 |
| MN10 | Tj-CT | 426.8 | 0.7561 | 0.1704 | 0.5857 | 0.0100 | 0.1503 | 0.1906 |
| | Tj-VP | 757.0 | 0.7091 | 0.2451 | 0.4640 | 0.0108 | 0.2235 | 0.2667 |
| | CT-VP | 503.5 | 0.6552 | 0.1878 | 0.4674 | 0.0089 | 0.1699 | 0.2056 |
| MN11 | CT-Lv | 313.9 | 0.5600 | 0.1449 | 0.4151 | 0.0126 | 0.1195 | 0.1703 |
| MN13 | CT-Lv | 313.9 | 0.6585 | 0.1449 | 0.5136 | 0.0126 | 0.1195 | 0.1703 |
| MN17 | Lv-Bt | 259.4 | 0.8889 | 0.1326 | 0.7563 | 0.0141 | 0.1042 | 0.1610 |

However, as previously stated, this assumption may not be true at small scales, a pattern that may include several local isolation events. Moreover, during the referred period there have been important geomorphologic changes, including four orogenic events (see Pickford and Morales 1994), that have not been taken into account in our analysis, due to the lack of GIS information on past geomorphology. Thus, actual d_{con} scores between basins could have been different during the past, being these geomorphologic differences part of the explanation for the observed lack of relationship.

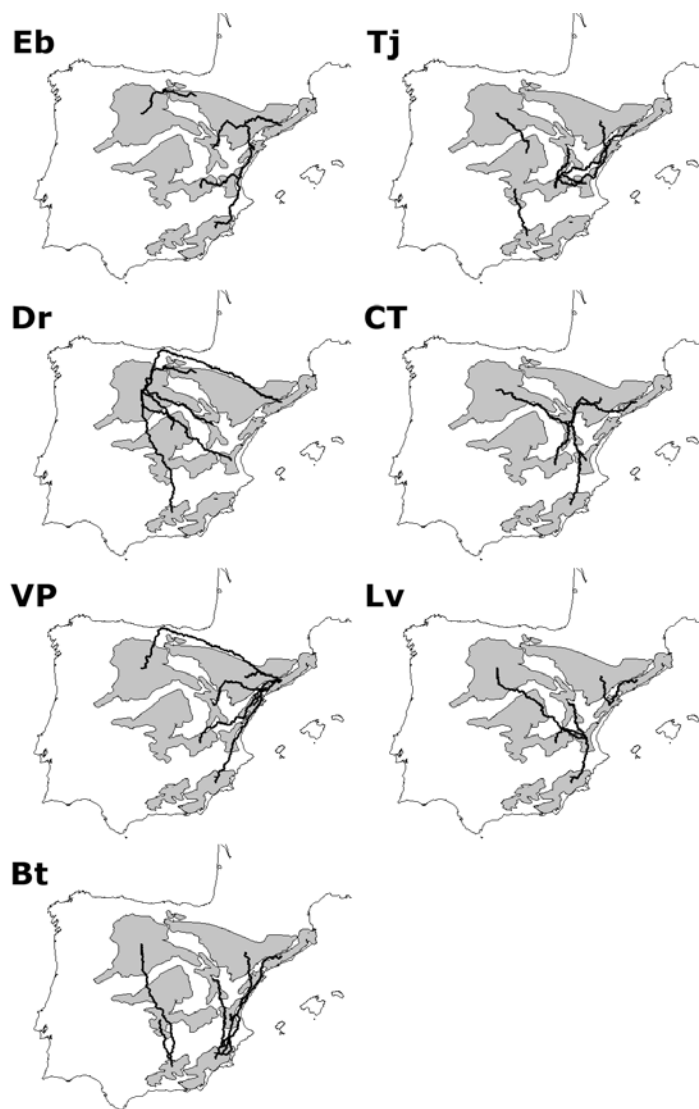


Fig. 6. Spatial location of the minimum cost pathways calculated for the movement among the centroids of the sedimentary basins (see text). Basin codes as in Figure 5

Interestingly, this is consistent with the lack of correlation between the scores of the connectivity distance between pairs of basins (d_{con}), and their corresponding β_w observed scores (Spearman $r = -0.2957$; $N = 19$; $t_{(N-2)} = -1.2761$; $p = 0.2190$). As the correlation between d_{con} and the results of the model used to calculate β_w predicted scores is 1, the figures of the correlation are the same from those of the correlation observed and predicted β_w scores).

Currently we have no way to assess how this lack of relationship is due to differences in the connectivity among areas in the past, or to other differences in the studied faunas (see below). Thus, new data and/or good-quality extrapolations about the physical geography of the Iberian Peninsula are needed to unravel this Gordian knot. Latter analyses should try to overcome this drawback.

Together with the abovementioned geomorphologic changes, it is important to take also into account another two issues. On the one hand, the time averaging effect implicit in the use of biozones with large time extent may also play a fundamental role in such pattern. On the other, climatic variability through time and adaptive differences between different groups of mammals could be avoiding the extrapolation of recent patterns to the past (see further insights below).

The lack of relationship between β_w -diversity and connectivity, suggests that other factors not present in recent times were affecting Neogene mammal faunas. Since we have not included any proxy for environmental connectivity in our database a higher environmental diversity between sedimentary basins that is observed today is a possible explanation. Ecological barriers, not only topographical barriers, may produce isolation between sedimentary basins and promote divergence in their pool of species, thus leading to higher β_w -diversity values.

As a matter of fact, previous analyses have revealed increasing evidence of a variable heterogeneity of the faunas across the recorded sedimentary basins (Agustí 1999, Morales et al. 1999, Nieto et al. 2003). These differences can be recognized in many periods along the Neogene record of Spain but there are also several periods when faunal differences between basins seem to disappear. Heterogeneity and its temporal changes have been related to variation in environmental heterogeneity (Agustí 1999) but also it has been suggested that immigration events may have also affected the degree of heterogeneity.

Variations in β_w -diversity throughout the Neogene and significant climatic and migratory events are summarised in Figure 7. Although this pattern is obviously affected by the nature of our data, some tentative interpretations may be proposed. According to Agustí (1999), regional

heterogeneity was established early in the Miocene, around 19 Ma. (MN3) when strong differences in the faunas can be appreciated between the Mediterranean basins and the interior basins.

Our results contrast with this hypothesis, since a low β_w -value is observed during MN3. As mentioned by us elsewhere (Nieto et al. 2003), these differences in the results may be caused by a poor record. MN3 is marked by an immigration event characterized by the arrival of the North American equid *Anchitherium* although the effects of this event are not reflected in our results.

On the contrary, the *Gomphotherium* landbridge (the connexion between Africa and Eurasia that caused a large faunal interchange, the *Gomphotherium* event), during the MN4, is associated with a high mean β_w -value and high variance.

Other immigration events are also associated with high β_w figures, like the immigration flow between North America and Eurasia during the MN9 (arrival of *Hipparion*) and between Africa and Eurasia during the Messinian Crisis (MN13).

The temperature and humidity curves proposed by Calvo et al. (1993) point out the relationship between climatic changes and changes in β -diversity. As can be seen in Figure 7, β -diversity follows the changes in the temperature curve during much of Early and Middle Miocene. High β -diversity scores coincide with the warm periods of MN4, MN5, MN9 and MN10, whilst low figures are found in the colder MN3 and MN6. However, this relationship is far from clear, with MN2 presenting high β -diversity despite its cold climate.

In contrast, the warm conditions on MN11 are linked to a low β -diversity, although this fact might be explained by the aridity of this period, which resulted in a generalization of savannah environment throughout all the Iberian Peninsula (Morales et al. 1999). However, despite its similar arid and warm conditions, MN5 presents high β -diversity figures, questioning the previous interpretation. It seems that different factors related to climate and migrations interact in a complex way to determine the observed patterns of β -diversity changes through time.

At the same time, the observed patterns may be affected by differences in the completeness of the fossil record. This also applies to the extreme β -diversity value of MN17, which can not be interpreted and should be supposed to be the result of their poor record, restricted to few localities.

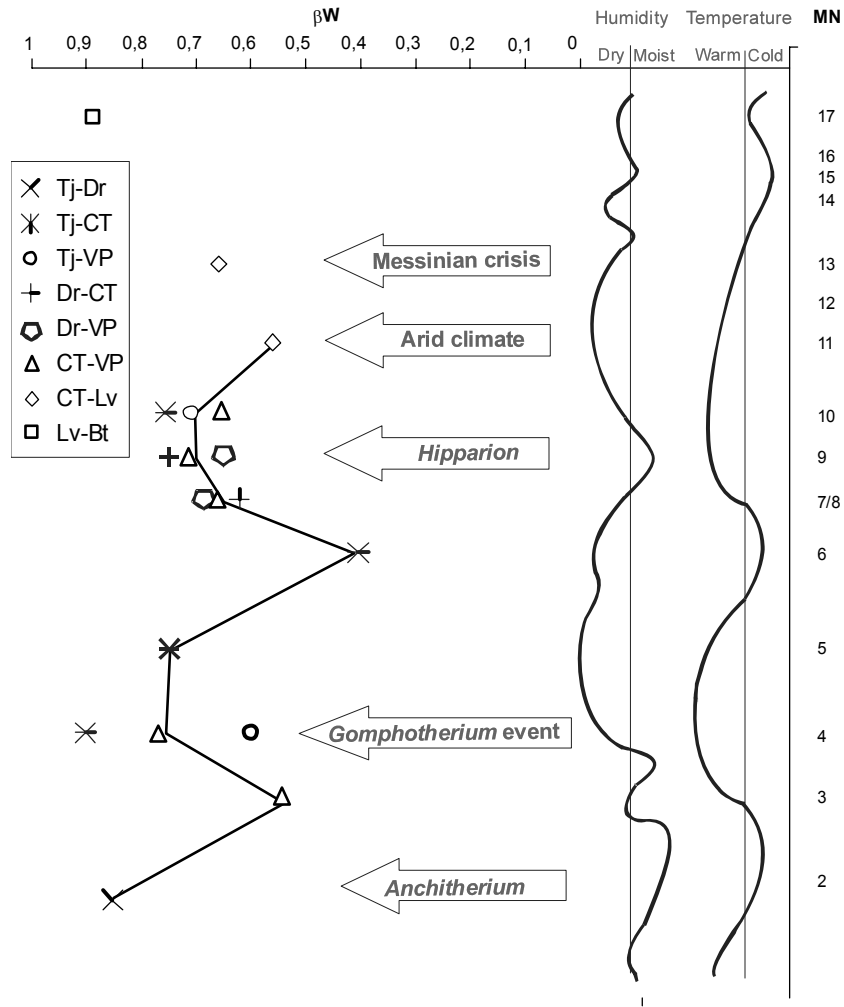


Fig. 7. Variations in β_w between basins throughout the Neogene, and significant climatic and migratory events. Continuous line connects mean values. Basin codes for the basins as in Figure 5. Palaeoclimatic humidity and temperature curves modified from Calvo et al. (1993)

10.5 Further insights

Our results from recent faunas show the importance of connectivity, and thus of species migration between areas, on the patterns of species replacement. Although the analysis here developed is partial and still preliminary, differences in environmental conditions seem to play a secondary role in the faunistic change between areas of the Iberian Peninsula in the present, when connectivity issues are taken into account. This should not be a surprise, as other authors have found inter-area migration to have an important effect on species replacement. As Duivenvoorden et al. (2002) state, a correct implementation of dispersal influence into the analyses of biodiversity patterns produces variations in the description of the factors affecting its geographic distribution. This aspect should be integrated into further macroecological work. Today, GIS tools provide a good method to describe patterns of connectivity (Verbeylen et al. 2003, Nikolakaki 2004, this work), or biological migrations and invasions (e.g. Macdonald and Rushton 2003, Dark 2004, Wiegand et al. 2004, Ming and Albrecht 2004), and new tools are developed to assess and analyze distance matrices (see Ferrier 2002), so it is time to have a new look to the patterns of β_w , using an spatially-explicit point of view.

Although our knowledge about mammal Neogene faunas is incomplete and spatial and temporally biased (see Nieto et al. 2003), several aspects arose from the developed analysis. No relationship can be appreciated between topographical connectivity and β -diversity among regions during the Neogene, despite they are highly correlated in the present. Higher β -diversity episodes seems to be related to major immigration events, which may affect different basins in a differential way, while lower β -diversity may be associated with environmental homogeneity, in opposition to recent pattern, where habitat and environment were less important. Although a test of our model using more complete checklists for past faunas is highly desirable, these kind of analyses are probably not affordable with present state of knowledge (past temporal resolution and geomorphologic data).

Therefore, more complete analyses on the relationship between faunistic and environmental differences in the present are also needed to confirm the here-found pattern of the dependence of β -diversity on connectivity. Among these analyses, the role of spatial distance *per se* should be evaluated, separating its effects from the purely attributable to connectivity-mediated distances. On the other hand, as mentioned before, the role of geomorphology may not be constant i) through time (varying

due to climatic variation and geomorphologic changes; see Morales and Pickford 1994), and ii) in different groups of species (with different bioclimatic requirements). According to the first statement of this dichotomy, it would be advisable for further investigations to make an effort to develop better estimations on the connectivity distance between basins during the past. This includes the development of fine grain estimations of the geomorphologic configuration of the Iberian Peninsula at different time periods. Following the second statement, more precise studies of the role of connectivity on species dispersal should focus on the response of groups of species with similar bioclimatic requirements (e.g., dry-Mediterranean shrubland species, temperate forest species or Mediterranean forest species) to different climatic scenarios (glacial maximums, warm interludes, etc.). Today, we have a good knowledge on the environmental requirements of the Iberian Holocene mammal species, as well as good scenarios of the climatic and landscape variations through that period, as well as for future climatic changes. Before obtaining a knowledge good enough as to determine the role of connectivity in shaping Neogene faunas, the Quaternary seems to be a good benchmark to test its role through the past and today. The rich mammal fossil record of the European Quaternary may be a good target for such an study. Geomorphology may be considered constant for the last million years, being the single major factor affecting connectivity during the Pleistocene the eustatic changes in sea level, a variable that may be easily included in a GIS environment from topographic maps of land and seafloor elevation. Including these data will give temporal continuity to present analyses, maybe helping to understand the lack of agreement between recent and Neogene patterns. Moreover, the existence of several records for different time-periods during the last century (see an example at Araújo et al. 2004) may help us to investigate up to what point it is possible to extrapolate distributions from one time to another using connectivity, as well as to determine the importance of connectivity in modifying the purely environmentally-induced patterns in the distribution of single species and entire communities.

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