



An evaluation of the influence of environment and biogeography on community structure: the case of Holarctic mammals

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ABSTRACT

Aim To evaluate the influence of environment and biogeographical region, as a proxy for historical influence, on the ecological structure of Holarctic communities from similar environments. It is assumed that similarities among communities from similar environments in different realms are the result of convergence, whereas their differences are interpreted as being due to different historical processes.

Location Holarctic realm, North America and Eurasia above 25° N.

Methods Checklists of mammalian species occurring in 96 Holarctic localities were collected from published sources. Species were assigned to one of 20 functional groups defined by diet, body size and three-dimensional use of space. The matrix composed of the frequencies of functional groups in the 96 localities is used as input data in a correspondence analysis (CA). The localities are classified into nine groups according to Bailey's ecoregions (used as a surrogate of regional climate), and the positions of the communities in the dimensions of the CA are compared in relation to ecoregion and realm. Partial regression was used to test for the relative influence of ecoregion and realm over each dimension and to evaluate the effect of biogeographical realm on the variation in the factor scores of the communities of the same ecoregion.

Results In some cases, mammalian communities from areas with similar regional climates exhibit convergence in community structure, irrespective of the biogeographical realm where they are located. However, all of them are clearly subdivided into Nearctic and Palearctic subsets. Differences in the composition of the regional pools only partially explain differences in local communities between realms.

Main conclusions Holarctic mammalian communities from regions with widely different climates differ in ecological structure irrespective of their biogeographical location. On the other hand, the structures of Nearctic and Palearctic communities from regions of similar climate radically differ in some features. Thus, although present climatic conditions influence community structure, contingent historic processes associated with each region also play a major role in determining community structure.

Keywords

Biogeographical regions, community convergence, community structure, ecoregions, environmental factors, Holarctic mammal communities, regional historical processes.

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INTRODUCTION

Knowledge of the structure of communities and the factors that determine it is basic to understanding the dynamics of ecological communities (Jernvall & Fortelius, 2004). Community structure can be described by different parameters, such as species richness or functional group composition. Many researchers have focused on the patterns of variation of species richness at the continental scale trying to relate them to environmental (Pagel *et al.*, 1991; Danell *et al.*, 1996; Francis & Currie, 1998; H.-Acevedo & Currie, 2003) and historical factors (Latham & Ricklefs, 1993; McGlone, 1996; Ricklefs, 2004). Comparison of the ecological structure of local communities and their relationship to environment and history is related to the controversial concept of community convergence (Cody & Mooney, 1978; Crowder, 1980; Fuentes, 1980; Blondel *et al.*, 1984; Blondel, 1991; Losos, 1992), although ecologists have paid little attention to this topic in recent years. However, the concept of community structure has been adopted by mammalian palaeoecologists, becoming the conceptual basis for several studies (Shipman, 1986; Legendre, 1989; Andrews, 1990; de Bonis *et al.*, 1992; Ducrocq *et al.*, 1994; Gibernau & Montuire, 1996; Sen *et al.*, 1998; Croft, 2001; Rodríguez, 2001; Montuire & Marcolini, 2002), although rarely as explicitly recognized as in the extensive methodological review by Andrews (1996). Thus, during the last decade the analysis and comparison of the structure of recent mammalian communities has been almost the exclusive preserve of palaeoecologists as a way to extract 'rules' or general patterns from the present that can be extrapolated to the past. Some studies focus on regional variation in the distribution of ecological types of species and their relationship to environmental factors (Andrews & O'Brien, 2000; Badgley & Fox, 2000), whereas others take local communities as their unit of analysis (Rodríguez, 1999).

Samuels & Drake (1997) consider community structure to be the result of multiple interactions between species in time and space, constrained by the environment and chance events. Environment is thought to determine community structure because, in the short run, it delimits possible configurations and, over evolutionary time, it determines the evolutionary trends of species leading to the appearance of ecologically similar species in environmentally similar areas (Samuels & Drake, 1997). On the other hand, history comprises the so-called 'chance events' like the order of arrival of species, although it is not restricted to them. Historical processes occurring in evolutionary time determine the regional pool of species, a key factor in determining community structure (Ricklefs, 1987, 2004; Huston, 1999; Godfray & Lawton, 2001; Mouquet *et al.*, 2003). Certainly, the evolution of the regional pool is influenced by climate and other environmental factors on a large time-scale, along with chance events, leading to a complex interaction of the main factors involved in the development of community structure.

The aim of this paper is to evaluate the influence of habitat type and biogeography, as proxies for the effects of environ-

mental and historical influences, on the ecological structure of Palearctic and Nearctic communities. It is assumed that similarities among communities from similar environments in different realms are the result of community convergence, whereas differences are interpreted as being related to different historical processes. Ideally, to test the influence of history on community structure we need to know the processes of assembly of particular communities and to evaluate to what extent the differences in their history explain their differences in structure. However, since such information is not available, the alternative is to use biogeography or the spatial structure of the variations in community structure not related to environmental factors as a proxy for history (see e.g. Hawkins & Porter, 2003a; Hawkins *et al.*, 2003a; Svenning & Skov, 2005). The rationale is that communities in the same biogeographical region (equivalent to a continent at the scale of the present analysis) share a broadly similar history, unique to that continent. So, differences in community structure among communities from the same environment in different continents should be the result of historic processes. Certainly this approach does not account for all historical influences, since every community has its own history that may partially explain differences in structure among communities of the same continent and environment. However, quantifying the biogeographical output on the structure of communities provides indirect evidence of the relative importance of historical modifications on regional faunas.

In this study we compare local communities from two regions of similar latitudinal position, which present comparable environments. The mammalian faunas from both regions have a long separated history punctuated by several faunal interchanges. Since 30 Ma such interchanges took place across the Bering Strait, which acted as a more or less selective filter (see the review by Cox, 2000). The most intense interchanges were recorded during the Pleistocene, although they were restricted to large cold-tolerant species which could pass the Bering Strait during glacial times. Holarctic faunas became more homogeneous, but the closure of the strait 14,000–15,000 years ago and the macrofaunal extinctions that strongly affected the Nearctic between 15,000 and 10,000 years ago (Stuart, 1991) produced increasing differences between the realms. As a consequence, both regions are broadly similar at family level (80% of the species belong to the 15 families shared between both regions) but they have strong differences at lower taxonomic levels (they share only 20 genera out of 227). High-level taxonomic similarity implies functional similarity and thus may reduce the effect of history on the regional pool due to the presence of the same functional types in both regions. However, differences at low taxonomic levels may also go hand in hand with some degree of functional dissimilarity, reinforcing the role of the evolutionary history of each region in shaping its regional pool. In fact, the functional distribution of the species within the different families shows a mixture of both trends (see Fig. S1 in Supplementary Material). Shared families tend to have the same functional types in both regions, but they differ in species richness and in the

proportion of each functional type. There are also several non-shared families which may cause differences in features of local communities, even when they contain relatively few species. For example, the distribution of the Bovidae, present in Africa but absent in South America, may explain the differences in species richness between the savannas from both continents (Nieto *et al.*, 2005). As a whole, it is evident that the mammalian faunas of both regions are the result of complex, not completely independent, evolutionary histories. To what extent their differences determine the structure of local communities will be analysed in this study, while the similarities can be considered the result of community convergences related to similar responses to variations in environmental factors.

It is beyond the scope of this paper to discuss the community concept in detail (see McIntosh, 1995 for a review), but for the sake of clarity a definition of our unit of analysis is needed. We use the term ‘mammalian community’ to designate all the species actually occurring in a given area. Since most of the communities analysed here are from protected areas, their boundaries are in practice determined by the limits of the reserve. We are aware that this definition can be criticized on the grounds that it only takes into account a subset of the species actually occurring in the area, i.e. the mammals, or that it overestimates the number of species actually interacting. Despite these drawbacks we feel that this is a useful approach to the evaluation of the influence of different factors on community structure.

THE DATA BASE

Species lists of terrestrial mammals from 96 Holarctic localities were collected from published sources (see Table S1 in Supplementary Material and Fig. 1). The area of study was restricted to Eurasia and North America above 25° N, roughly coinciding with the limits of the Holarctic realm, excluding North Africa. The faunal lists for these localities were selected according to the criteria detailed in Rodríguez (2004).

Chiroptera, domestic and exotic species have been removed from the lists.

Bailey’s ecoregions (see description in Bailey, 1996) have been used as a proxy for environmental factors. This worldwide hierarchical classification system regionalizes the continents in areas of similar climate, vegetation structure and soil, regardless of biogeographical differences in species composition. The GIS version of Bailey’s *Ecoregions of the Continents* (Bailey, 1989/1993) is available at the Global Ecosystems Database (Version-II; <http://www.ngdc.noaa.gov/seg/ecosys/ged.shtml>, last access 25 August 2005). Bailey’s classification consists of four ecological levels: domains, divisions, provinces and sections. Domains are extremely broad areas, defined by the prevailing climate, and are broken down into divisions according to further climatic criteria. Provinces and sections are lower-rank categories defined according to the dominant plant formations in the area. As a general rule, it would be desirable to select the smaller and more precise categories as the unit of analysis. However, taking into account the global scale of our analysis, selecting a low-rank category would result in very few localities in each category, reducing statistical power. Consequently, we have chosen Bailey’s division category as the unit of analysis, since it encompasses moderately wide areas well represented in both Eurasia and North America and they have been useful in similar analyses (J. Rodríguez, unpubl. data; J. Hortal, J. Rodríguez, M. Nieto & J. M. Lobo, unpubl. data). The 96 localities selected are located in nine divisions (Fig. 1); these divisions encompass around 55% of the area of the two regions.

METHODS

Community structure is represented here by the number of species in 20 functional groups (Table 1). These groups are described in detail in Rodríguez (2004). They are based on a combination of body size, trophic habits and utilization of the three-dimensional space by the mammalian species. The use of these categories allows comparison of the ecological structure of communities from different realms or time periods.

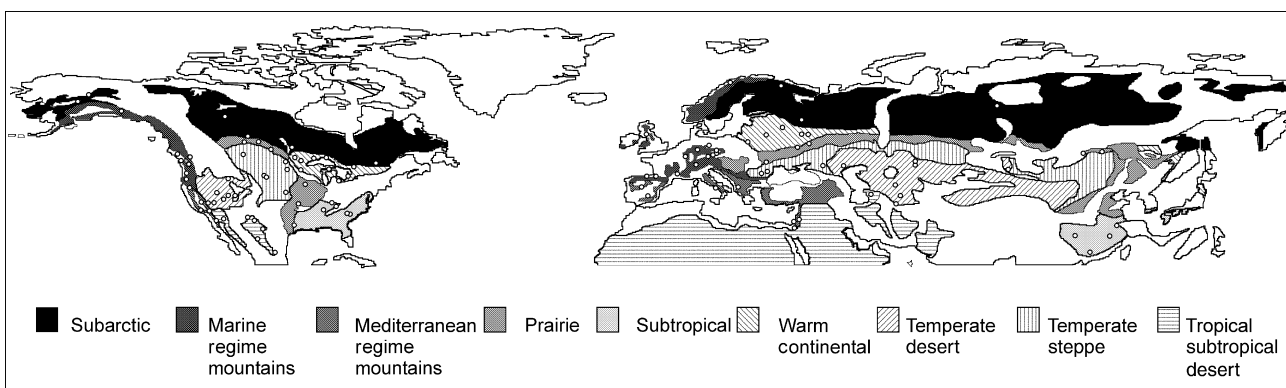


Figure 1 Geographical location of the 96 localities analysed and boundaries of the Bailey’s ecological divisions in which they are located. Redrawn from Bailey (1989/1993) (available at the Global Ecosystems Database Version-II; <http://www.ngdc.noaa.gov/seg/ecosys/ged.shtml>, last accessed 25 August 2005), using geodetic coordinates (no projection; WGS1984 datum).

Table 1 Ecological categories used to classify mammalian species into functional groups

Code	Name	Definition
AqP	Aquatic predator	Predates on aquatic vertebrates and invertebrates
STP	Small terrestrial predator	Predates on terrestrial vertebrates and birds. Its diet may include invertebrates. Body weight below 30 kg
LTP	Large terrestrial predator	Predates on terrestrial vertebrates, usually mammals. Body weight over 30 kg
ArP	Arboreal predator	Arboreal or semi-arboreal. Predates on tree dwelling vertebrates and invertebrates
AqPI	Aquatic predator of invertebrates	Aquatic predator. Feeds only on invertebrate species
StPI	Subterranean predator of invertebrates	Lives underground. Exhibits morphological adaptations to dig galleries. Feeds underground on invertebrate species
LTPi	Large terrestrial predator of invertebrates	Terrestrial. Feeds on invertebrates. Body weight over 10 kg
STPI	Small terrestrial predator of invertebrates	Terrestrial. Feeds on invertebrates. Body weight below 10 kg
STOm	Small terrestrial omnivore	Terrestrial. The diet includes a variety of plant food, as well as invertebrates and even small vertebrates. Body weight below 1 kg
LTOm	Large terrestrial omnivore	Terrestrial. Feeds on a variety of vegetable food, invertebrates and small vertebrates. Body weight over 1 kg
AOM	Arboreal omnivore	Arboreal. Feeds on seeds, fruit, leaves and invertebrates. Its diet may include small vertebrates and eggs
STHb	Small terrestrial herbivore	Terrestrial. Feeds on plant material. Seeds are usually an important part of the diet. Body weight below 1 kg
SFgFrm	Small-sized foregut fermenter	Ruminant. Body weight below 40 kg. Feeds mainly or exclusively on vegetables
MFgFrm	Medium-sized foregut fermenter	Ruminant. Body weight between 40 and 200 kg
LFgFrm	Large-sized foregut fermenter	Ruminant. Body weight over 200 kg
SHgFrm	Small-sized hindgut fermenter	Non-ruminant. Body weight below 40 kg. Feeds mainly or exclusively on vegetables
LHgFrm	Large-sized hindgut fermenter	Non-ruminant. Body weight over 200 kg
StHb	Subterranean herbivore	Lives underground. Exhibits morphological adaptations to dig galleries. Feeds underground on roots, bulbs, etc.
ArHb	Arboreal herbivore	Arboreal. Feeds on trees and its diet may include leaves, twigs, buds, flowers, fruits and seeds in variable proportions
AqHb	Aquatic herbivore	Aquatic adapted for swimming. Feeds mainly on vegetable food

The 96 localities vary widely in area, ranging from 10 to 440,000 km². Before further analysis, we tested the effect of area on the richness of each ecological group. Only three variables are marginally correlated with area (large terrestrial omnivores, arboreal omnivores and small terrestrial herbivores) according to the Spearman's test, and two have negative coefficients (v_{12} : $R = -0.22$, $N = 96$, $P = 0.029$; v_{13} : $R = -0.21$, $N = 96$, $P = 0.038$; v_{14} : $R = 0.29$, $N = 96$, $P = 0.004$). In addition, this result is due to the influence of two outliers. Although this lack of correlation between area and richness may seem unexpected, it is consistent with previous results indicating that at the macroscale (continent-wide or planetary) environment and history are far more important than area in determining species richness (Rohde, 1998; Hawkins & Porter, 2001, 2003b; Rodríguez *et al.*, 2004; J. Hortal, J. Rodríguez, M. Nieto & J. M. Lobo, unpubl. data). We also found that there are no significant differences in the size of the localities between the two realms ($t = -1.59$; d.f. = 94, $N = 96$, $P = 0.114$). Nonetheless, such a large variation in area of study units makes it necessary to take area explicitly into account prior to any analysis of species richness using such kinds of data.

We conducted a correspondence analysis to reduce the number of variables (ecological groups) for subsequent analyses. The input matrix contained the number of species in the 20 functional groups (see Table S2 in Supplementary Material). Therefore, the structure of a community is represented here by its position in a multidimensional space determined by the frequency of species in each functional group (Rodríguez, 2004). The closer two communities are in the multidimensional space, the more similar are their structures. If convergence in the ecological structure of communities exists, they will cluster in the multidimensional ecospace by ecological division, irrespective of their geographical position (Palearctic vs. Nearctic). In contrast, biogeographical effects will cause communities of the same division from different continents to have different structures, and thus they will be split by continent in at least one of the dimensions. This effect was quantified using a general linear model (GLM), assuming a normal distribution for the values of the communities in the dimensions, and using identity as the link function (see Dobson, 1999). Biogeographical region (Rbg) and Bailey's division (DvB) were used as binary predictor and multinomial predictors, respectively.

We used partial regressions to test the influence of Baileys' division (DvB), as a proxy for environment, and biogeographical realm (Rbg), as a proxy for history, over each dimension (see Legendre & Legendre, 1998 for the method, and some examples in Lobo *et al.*, 2001, 2002; Hawkins & Porter, 2003c; Hawkins *et al.*, 2003a; Nieto *et al.*, 2005). Here, to calculate the variability in each dimension that is independent from Rbg, but is related to DvB, we first regressed Rbg over DvB (using a multinomial distribution for DvB, and a logit function), and then used the prediction residuals (rDvB) as a predictor of the variability. The same process was used to calculate the variability in each dimension that is independent from DvB but is related to Rbg (using a binomial distribution for Rbg, and a logit function). As the effects of regional species pool over local faunas may differ at each kind of habitat, we also examined the effect of biogeographical realm on the variation of the factor scores of the communities from the same division on each dimension. This provided a finer evaluation of how and where differences in the regional species pool are operating. All analyses were carried out with GLM in STATISTICA (StatSoft, 2001).

RESULTS

Definition of the ecospace axes

Results of the correspondence analysis are summarized in Table 2. Six dimensions, accounting for 72% of total inertia, were retained after examining a scree plot of the eigenvalues. The first dimension separates temperate steppe and desert/semi-desert localities from the rest, based on the richness of large insectivores, small ruminants and large non-ruminant herbivore species in the former localities. Dimension 2 (D2) is dominated by the number of large insectivores and small ruminants, and clearly separates the three Palearctic localities of the subtropical division. Dimension 3 identifies a gradient according to the number of large terrestrial non-ruminant herbivores, small ruminants and aquatic invertebrate predators at one extreme, and arboreal predators and large insectivores on the other. Large herbivores and insectivores also show extreme coordinates in dimensions 4 and 6.

Partial regression: evaluation of environmental and biogeographical effects

Ecological division explained more than 65% of the variation in dimension 1, whereas biogeographical realm accounted for 49% of the variation in dimension 3. The variability explained for the remaining four dimensions was considerably lower (the unexplained variability ranged from 63.8% to 85.3%; see Table 3 and Fig. 2). However, the independent effect of Bailey's divisions on ecological structure was important for all dimensions except D3 (ranging from 14.4% to 65.4%), whilst the effect of the biogeographical realm was more important only for dimension 3. The joint effects of both DvB and Rbg were negligible in all cases (see Fig. 2).

Table 2 Results of the correspondence analysis using the number of species of each functional group per locality as the input matrix. D1, ..., D6 are the six dimensions identified (i.e. gradients of community structure variation). Cum.% of inertia is the cumulative percentage of inertia. Functional group coordinates represent the location of each functional group in the ordination space defined by the six new dimensions (i.e. their contribution to the retained dimensions)

	D1	D2	D3	D4	D5	D6
Eigenvalue	0.11	0.092	0.043	0.036	0.024	0.021
% of inertia	24.415	20.476	9.633	7.952	5.332	4.608
Cum.% of inertia	24.41	44.89	54.52	62.48	67.81	72.42
Functional group coordinates						
AqP	-0.458	0.215	-0.205	0.129	-0.118	0.344
STP	-0.097	-0.038	-0.075	0.136	-0.045	-0.088
LTP	0.165	0.26	0.084	0.354	-0.046	0.155
ArP	-0.181	1.238	0.621	-0.006	-0.232	0.081
AqPI	-0.681	-0.089	-0.776	-0.306	-0.16	-0.051
StPI	-0.352	0.143	-0.531	-0.573	0.232	-0.265
LTPI	1.407	3.837	0.494	-1.103	-0.23	0.467
STPI	-0.29	0.005	-0.111	-0.111	-0.015	-0.086
STOm	0.12	0.002	-0.043	-0.075	-0.041	0.143
LTOm	0.046	0.04	-0.014	-0.087	0.2	0.123
AOm	-0.177	0.222	0.126	-0.256	0.259	0.09
STHb	0.457	-0.296	0.061	-0.076	-0.134	0.031
SFgFrm	1.921	1.907	-0.95	0.102	-0.106	-0.662
MFgFrm	-0.021	-0.17	0.19	0.157	0.086	-0.263
LFgFrm	-0.45	0.013	-0.126	0.672	-0.28	0.164
SHgFrm	0.093	-0.093	0.265	0.095	0.078	-0.127
LHgFrm	1.336	-0.055	-1.298	1.686	1.885	0.661
StHb	0.542	-0.524	0.129	-0.252	0.138	-0.047
ArHb	-0.417	0.179	0.267	0.008	0.188	-0.111
AqHb	-0.438	-0.079	-0.094	0.071	-0.142	0.048

Position of communities in the multidimensional ecospace

The positions of the 96 communities in the six retained dimensions are plotted in Figs 3–5. In agreement with the partial regressions, communities are separated according to ecological divisions, in dimension 1. Subarctic, Marine Regime Mountains, Prairie, Subtropical and Warm Continental communities have negative scores in dimension 1, while Temperate Desert, Temperate Steppe and Tropical/Subtropical Desert communities have positive scores. However, there is a high degree of overlapping in the distribution of communities from different divisions so that it is impossible to separate them in many cases. For example, communities from the Mediterranean Division cannot be distinguished from those of the Warm Continental, Prairie or Subtropical Divisions in any dimension.

The GLM of the effect of biogeography on community structure found significant differences between Palearctic and Nearctic communities in at least one dimension for all divisions but two. Small sample sizes (five and six localities)

Table 3 GLM analyses used to partition the variation in the community structure dimensions. The variance explained in each dimension is calculated from the change in the deviance statistic from a null model, considering the explanatory qualitative variables with their respective code. To eliminate collinear interactions, we used partial regressions terms; each predictor variable was regressed against the other (e.g. DvB against Rbg), and the residuals of the resulting function were used as a new variable (in this case, rDvB) that represents the variability in each predictor that it is independent from the other (see text). Then, each dimension (D1, ..., D6) was modelled against these non-collinear partial regression terms to obtain the pure effects of DvB and Rbg (see Fig. 2). Dev is deviance, Ch.Dev is the change of deviance, and %exp is the percentage of explained deviance from that of the null model

	d.f.	Dev	Dev/d.f.	Ch.Dev	F	%exp
D1						
Null model	95	12.92	0.14			
DvB + Rbg	86	4.15	0.05	8.77	181.66	67.87
rDvB	87	4.82	0.06	8.1	146.38	62.72
rRbg	94	12.62	0.13	0.31	2.28	2.37
D2						
Null model	95	7.88	0.08			
DvB + Rbg	86	5.03	0.06	2.85	48.83	36.22
rDvB	87	5.37	0.06	2.51	40.73	31.89
rRbg	94	7.67	0.08	0.21	2.61	2.7
D3						
Null model	95	4.73	0.05			
DvB + Rbg	86	2.09	0.02	2.63	108.24	55.72
rDvB	87	4.43	0.05	0.3	5.81	6.26
rRbg	94	2.49	0.03	2.24	84.62	47.37
D4						
Null model	95	3.89	0.04			
DvB + Rbg	86	3.09	0.04	0.81	22.45	20.7
rDvB	87	3.18	0.04	0.71	19.53	18.33
rRbg	94	3.87	0.04	0.03	0.61	0.65
D5						
Null model	95	2.91	0.03			
DvB + Rbg	86	2.48	0.03	0.43	14.81	14.69
rDvB	87	2.48	0.03	0.42	14.77	14.51
rRbg	94	2.9	0.03	0.01	0.27	0.29
D6						
Null model	95	2.36	0.02			
DvB + Rbg	86	1.94	0.02	0.41	18.29	17.54
rDvB	87	2	0.02	0.36	15.73	15.32
rRbg	94	2.36	0.03	0	0.02	0.02

are probably responsible for the lack of significance, since the localities of both divisions may be clearly separated by realm in at least one dimension (Figs 3–5). Communities from the Subarctic division are separated in D1, D2 and D3; those from Marine Regime Mountains in D2 and D3; those from the Subtropical in D1, D2 and D5; those from the Warm Continental in D2, D3 and D6; those from the Temperate Desert in D2 and D3; those from Temperate Steppe in D3 and D4 and those from the Tropical/Subtropical Desert division in D2, D3 and D4. Using a $P = 0.05$ significance level, all

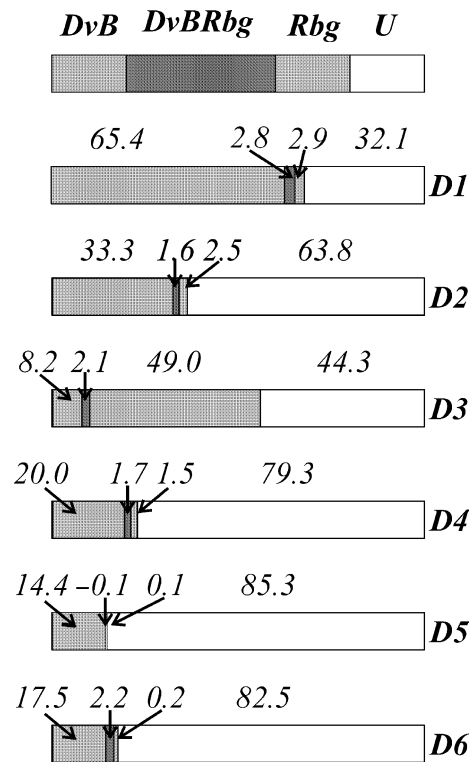


Figure 2 Results of the partial regression analyses used to evaluate the joint and independent influences of habitat and regional differences on community structure (see text). Bars represent the independent portions of influence over each community structure dimension (D1, ..., D6; see Table 2) of the following terms: the Bailey divisions (DvB), the biogeographical region (Rbg), their joint effects (DvB + Rbg), and the unexplained variation (U) (see Table 3).

dimensions found biogeographical differences in the structure of at least one division, although dimensions 2 and 3 are sufficient to identify the existence of differences between localities of the same division and different realms (Table 4 and Fig. 4).

Since there are differences in ecological structure between continents in virtually all divisions, it is important to determine if these differences are due to the same ecological groups of mammals irrespective of the ecological division of the locality. If this were the case, differences would be explained as a direct consequence of different regional pools. Results from both the partial regressions (Fig. 2) and division-by-division GLMs (Table 4), indicate that biogeographical effects are more evident in dimension 3. However, scatter plots (Fig. 4) indicate that there is no common pattern. Although Palearctic communities from Subarctic, Marine Regime Mountains, Prairie, Warm Continental, Temperate Desert, Temperate Steppe and Tropical/Subtropical divisions all have lower scores in dimension 3 than Nearctic communities, no clear ordination of Mediterranean Regime Mountain communities is observed in this dimension, and subtropical Palearctic communities have higher scores than the Nearctic ones. This

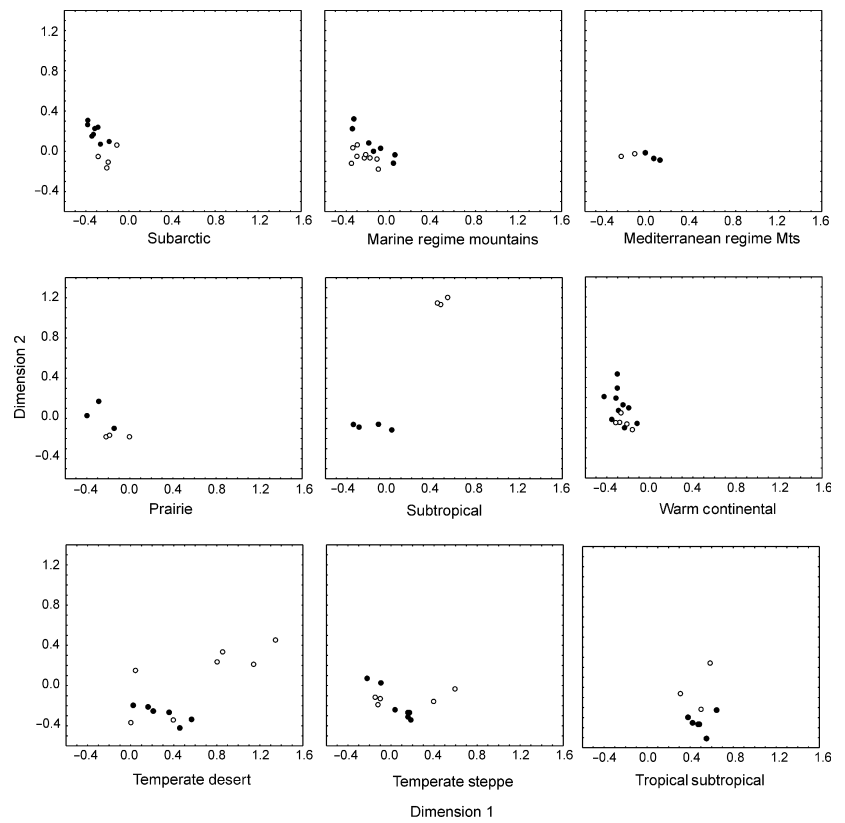


Figure 3 Position of the 96 communities in the first and second community structure dimensions (D1 and D2; see Table 2). Open circles, Palearctic Realm; black dots, Nearctic Realm.

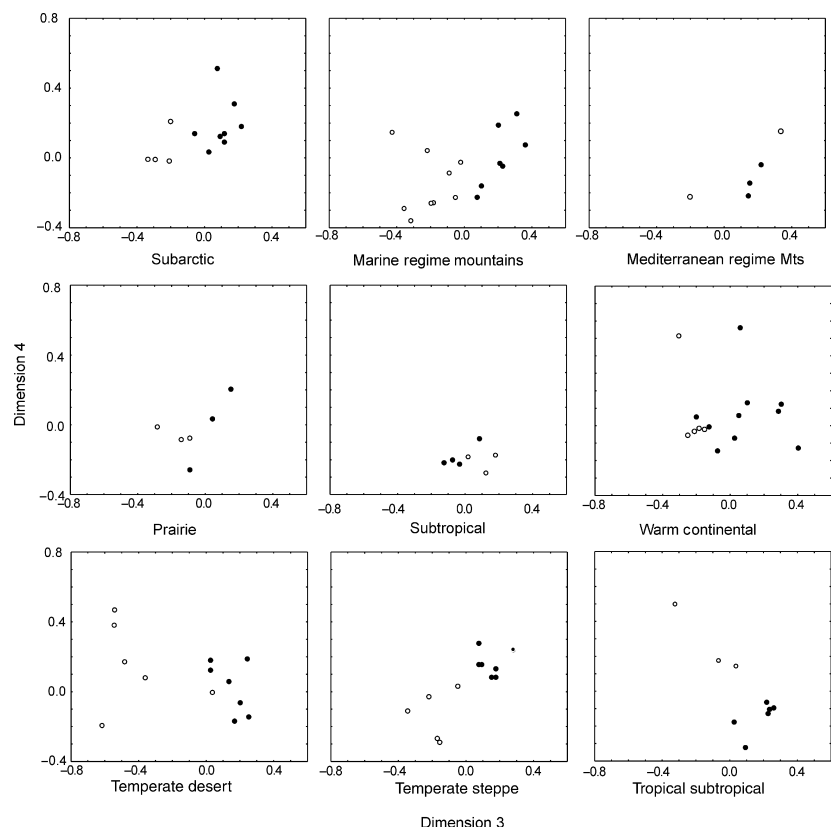


Figure 4 Position of the 96 communities in the third and fourth community structure dimensions (D3 and D4; see Table 2). Symbols as in Fig. 3.

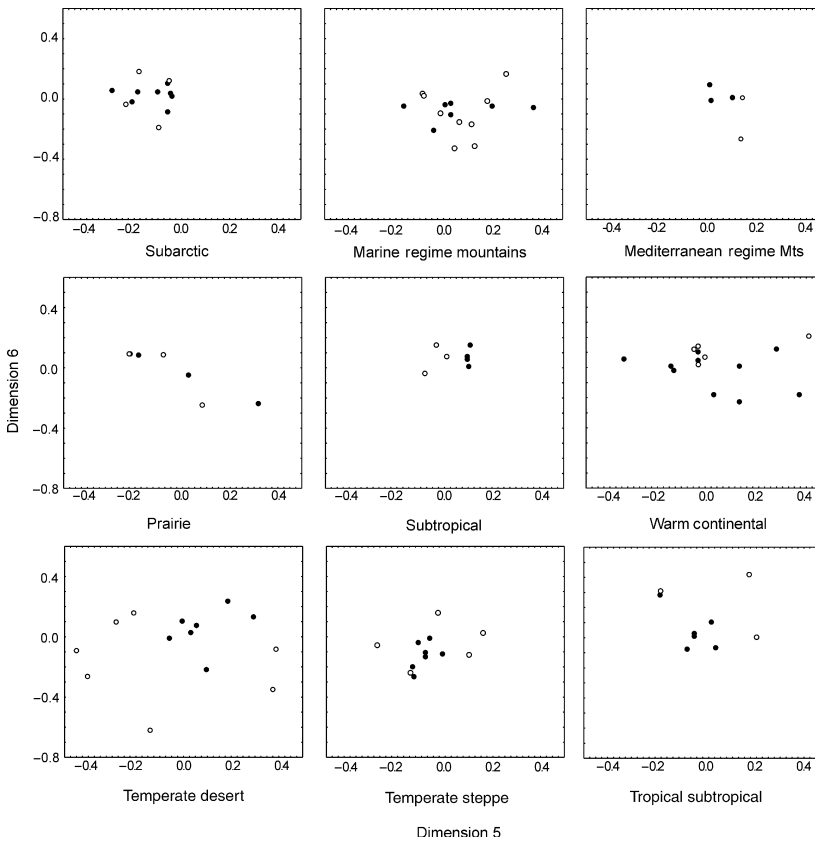


Figure 5 Position of the 96 communities in the fifth and sixth community structure dimensions (D5 and D6; see Table 2). Symbols as in Fig. 3.

Table 4 Results of the GLM analyses of the effects of biogeographical region over each habitat type. Numbers are the percentage of explained variability. Significant differences ($P < 0.05$) are in bold ($*P < 0.01$; $**P < 0.001$). The analyses used Rbg as a binary predictor for each dimension (D) at each Bailey division

Division	D1	D2	D3	D4	D5	D6
Subarctic	45.7	68.4**	83.3**	23.5	1.0	0.3
Marine Regime Mountains	11.5	28.0	74.2**	18.2	0.1	0.7
Mediterranean Regime Mountains	76.9	36.1	7.7	12.1	69.6	40.5
Prairie	42.3	61.6	55.3	3.0	12.7	2.3
Subtropical	89.4*	99.8**	47.3	7.9	88.4*	0.6
Warm Continental	4.3	27.3	44.9*	0.1	0.6	26.8
Temperate Desert	21.8	41.6	74.6**	2.6	13.5	23.0
Temperate Steppe	2.2	7.5	80.6**	70.1**	5.5	11.6
Tropical/Subtropical Desert	0.8	58.7	61.1	74.5*	16.6	29.0

reduces the amount of variance accounted for by biogeographical realm in the partial regressions (Fig. 2), but it is detected in the division-by-division analyses.

In order to evaluate the influence of differences in the regional species pools between the two biogeographical realms, the richness of species in each functional group in the Palearctic and Nearctic realms is compared, based mainly on Nowak (1991) (Fig. 6). It is noteworthy that the size of the two species pools is very similar (483 species in the Nearctic and

477 species in the Palearctic), especially since the Palearctic is roughly twice the area of the Nearctic. Although the general pattern is very similar in both regions, and also similar to the global pattern (J. Rodríguez, unpubl. data), significant differences exist between them ($\chi^2 = 76.307$; d.f. = 19; $P < 0.001$). Small terrestrial predators and small and medium-sized

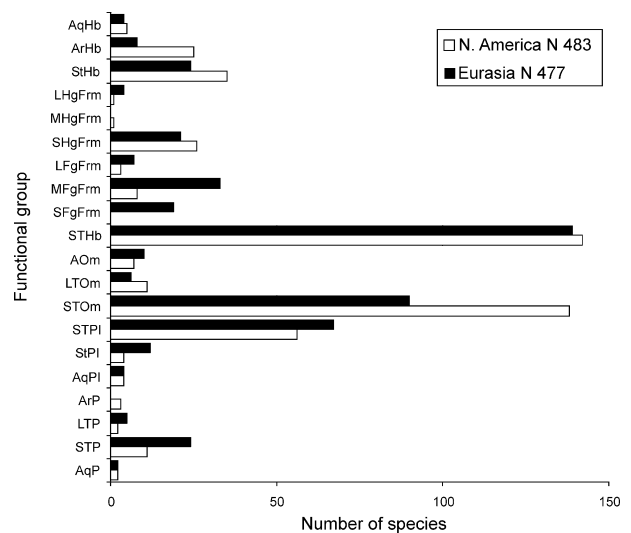


Figure 6 Number of mammalian species in the Nearctic and Palearctic species pools classified by ecological group (see Table 2).

ruminants are far richer in the Palearctic. In fact, small ruminants (below 40 kg) represented in the Palearctic by cervids and bovids, are absent from the Nearctic. In contrast, the number of arboreal and subterranean herbivores is greater in the Nearctic. Subterranean herbivores are represented in the Nearctic by the Geomyidae, while this role is played by the Muridae in the Palearctic. Another important difference is the large number of small omnivore species in the Nearctic. Undoubtedly, these differences in the regional pools are partially reflected in the composition of local communities. The number of medium and small-sized ruminants is a very important variable in dimensions 1–4 (Table 4), but none of the other groups play a major role in any dimension. Thus, a direct transposition of differences in the regional pool to differences in local community structure is not supported. Probably the strongest influence of the regional pool on the differences between communities of the same division relates to the number of small foregut fermenter species in the Subtropical division communities. Palearctic communities have three or four species, but this group is absent from the Nearctic.

DISCUSSION

Convergence and climate

Although in general mammalian communities from different ecological divisions, i.e. from areas with different regional climates and from both biogeographical realms considered together, tend to exhibit different community structure, in many cases differences in ecological structure between communities of different divisions were not found. Indeed, differences were detected only between communities from areas with extremely different climates. However, a more detailed comparison of the structure of those communities, including variables like daytime activity, social organization, more detailed resource-use characterization and many others, would perhaps detect additional differences between all divisions.

Fuentes (1976) defined community convergence not as the existence of identical or very similar structures in communities from different continents (as assumed by other authors; Blondel *et al.*, 1984; Ben-Moshe *et al.*, 2001), but as the existence of more similar structures in communities from similar environments in different continents than between nearby communities from different environments. This is a key distinction, since it allows historical or contingent factors to play a role in determining community structure, albeit a secondary one. Ordination of communities of two different realms in dimension 1 may be taken as evidence that, at the broad scale considered here, a certain degree of convergence in community structure does exist. This dimension separates desert and steppe communities from the rest (ANOVA, $F_{1,92} = 94.509$, $P < 0.001$). Such divisions are both characterized by high levels of water stress and a low complexity in vegetation structure, indicating that community convergence

is stronger when habitat conditions are extreme. However, although water availability is a well-known constraint for species richness (see review in Hawkins *et al.* 2003b), this community convergence pattern may not be matched by species richness figures. We find only weak (non-significant) differences in species richness between desert and steppe communities and the rest of the localities (ANOVA, $F_{1,92} = 2.372$, $P = 0.13$), and such differences are much less significant when the effect of the differences in area are controlled for species richness figures using partial regression (ANOVA, $F_{1,92} = 1.444$, $P = 0.70$). On the contrary, when the effect of species richness is eliminated from dimension 1 using the same technique, the separation between desert and steppe communities and the rest remains highly significant (ANOVA, $F_{1,92} = 87.823$, $P < 0.001$). Therefore, in this case, convergence in mammal communities of arid and subarid environments is not only a matter of limiting richness, but of a clear limitation of species assemblages according to habitat conditions (see also discussion in Cristoffer & Peres, 2003).

In spite of such convergence, it should be noted that differences in structure between communities from different divisions have rarely been detected. In many cases, communities from different divisions tend to have different community structure on average, but their distributions in the dimensions largely overlap, so it would be very difficult to assign a single community unequivocally to a particular division only on the grounds of its ecological structure. Therefore, we do not find a direct correspondence between climate and community structure. With the exception of extreme environments, the structure of mammal communities seems to be strongly affected by more factors than just habitat type.

Divergence and historical factors

Despite the tendency in the communities of the same division to cluster in multidimensional space, all of them can also be separated to some extent depending on their biogeographical provenance. Communities from the same division but different realms differ in mean scores per dimension, and, in many cases, are clearly split in two subsets according to biogeography in at least one dimension. Such differences cannot be directly predicted from differences in the species pool present in each realm, except in the cases where a particular group of species is completely absent in a biogeographical region. For example, the Palearctic hosts more medium-sized ruminant species than the Nearctic (30 vs. 8 species; see Fig. 6). Although, as would be expected, Nearctic Prairie division communities are poorer in this group of species (only one per community) than their Palearctic counterparts (two to five species), the opposite pattern appears in Temperate Steppe communities where three to six species of medium-sized ruminants are present in the Nearctic, and just two or less in the Palearctic (see Table S2 in Supplementary Material).

Although local factors can partially account for differences between communities both within and between regions, they

do not account for the general pattern observed. Previous analyses show that, at broad extents, the geographical patterns in mammal species richness are associated with variations in environmental conditions and water–energy dynamics (e.g. Currie, 1991; Andrews & O'Brien, 2000; Olff *et al.*, 2002; Tognelli & Kelt, 2004; see review in Hawkins & Porter, 2003b). Factors not included in Bailey's ecological divisions classification system account for faunistic particularities (e.g. mesoscale heterogeneity, topography, etc.; see Jetz & Rahbek, 2001; Rahbek & Graves, 2001). For example, two of the six medium-sized ruminants present in Yellowstone National Park, placed in a mountainous area, are closely associated with rough terrain (*Oreamnos americanus* and *Ovis canadensis*). Therefore it could be argued that local differences between the areas studied in both realms (not included in our analysis) could account for the differences in ecological structure between communities of the same division found in this study. Bailey's provinces could be used as a better proxy than division to explore such local effects, as they are based on the primary plant formations in the area. However, although most divisions can be subdivided into several provinces, these habitats are not always present and/or equivalent in both regions (Bailey, 1996). Therefore, in most cases Bailey provinces cannot be used for direct comparison of similar habitats between the two realms. However, it is worth mentioning that the major difference in community structure is observed between communities in the Subtropical division, despite all of them being included in the same province (Oceanic Mixed Constantly Humid Forests) in both the Nearctic and Palearctic realms. This suggests that although a more detailed characterization of the environment at the regional scale could provide a partial explanation for the differences between regions other factors are also operating.

Historic effects underlie the differences between the mammal faunas from both realms, thus accounting for an important part of the regional differentiation of community structure (Hawkins & Porter, 2003a; J. Hortal, J. Rodríguez, M. Nieto & J. M. Lobo, unpubl. data). Such regional differences affect the response of communities to local environmental factors (Ricklefs, 1987, 2004) at two levels: (1) influencing the regional species pools, due to limitations in the evolutionary solutions present (i.e. genera, families, etc.; e.g. Nieto *et al.*, 2005) and (2) through the assembly of local communities (Cornell & Lawton, 1992; Losos, 1992), by means of the *de novo* assemblage of communities in empty areas (e.g. Hawkins & Porter, 2003a), due to the effect of past environmental conditions (e.g. Hawkins *et al.*, 2005) or to the complex co-evolution between local species and their habitats (see Cristoffer & Peres, 2003).

The most obvious effect of the regional pool on community structure is the absence of a particular group of species (e.g. the absence of small-sized ruminants in the Nearctic or the absence of large hindgut fermenters in both regions). Such absences can be explained either because species with those characteristics never evolved or migrated into that realm or because they went extinct. As in the case of the differences

between Palaeotropical and Neotropical mammal communities (Nieto *et al.*, 2005), these absences produce strong differences between Palearctic and Nearctic communities. Large hindgut fermenters, like elephants and rhinos, occurred in both realms during the Miocene, but became extinct at the end of the Pleistocene (Stuart, 1982). Small ruminants, represented in the Palearctic by the genera *Gazella*, *Muntiacus*, *Moschus*, *Capreolus*, *Naemorhedus*, *Pantholops*, *Procapra* and *Saiga* (Nowak, 1991) were also present in the Nearctic during the Late Pleistocene, represented by species in the genera *Capromeryx*, and *Stockoceros* (Stuart, 1991). Climate or environmental change may have had a part in Late Pleistocene (or older) extinctions, as frequently argued (Guthrie, 1995; Beck, 1996), but this clearly represents a historical event rather than a current factor (see Hawkins *et al.*, 2005).

CONCLUDING REMARKS

Our results are congruent with the well-known principle that the environment plays a role in determining community structure (Blondel, 1991; Andrews, 1996; Ben-Moshe *et al.*, 2001). However, we have also shown that mammal communities with different structures exist in similar environments across the Holarctic. Although only a limited number of configurations are possible in a particular environment (see Lawton, 1999; Rodríguez, 2004), convergence between Palearctic and Nearctic communities is observed only in the case of extreme environments. Divergences in mammal community structure seem to be related to regional factors (this study) and the assembly of local communities (Rodríguez, 2004; unpubl. data). Thus, the inference of past environments through the comparison of fossil and recent faunas (e.g. Kay & Madden, 1997) should be reconsidered. Such an assumption paradoxically assumes that historical factors are time-independent, i.e. that the regional species pool, environmental conditions or community responses do not change through time inside the borders of a biogeographical realm. In the same way, the functional structure of recent communities should not be viewed as the direct outcome of current conditions, but as the outcome of both historical and habitat factors (see Hawkins & Mills, 1996; Lawton, 1999). Therefore, studies on community assemblage patterns should focus on the regional species pool available (Tofts & Silvertown, 2000; Hillebrand & Blenckner, 2002; Borges & Brown, 2004; Rodríguez *et al.*, 2004), as well as on the effects of current local conditions.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>:

Figure S1 Frequencies of functional group per realm.

Table S1 Data on localities included in the analyses.

Table S2 Input data for correspondence analysis.

BIOSKETCHES

Jesus Rodríguez is a palaeoecologist with research interests in macroecology and the factors influencing the assemblage of ecological communities. His research is focused on the evolution of Pleistocene European mammalian communities in relation to environmental and historic factors.

Joaquín Hortal's main research interest is the quantitative description of geographical patterns of biodiversity, as well as the factors underlying them. He is also interested in biodiversity estimators, conservation biogeography, predictive modelling and the ecology, evolution and biogeography of dung beetles. He is currently working on biodiversity patterns (especially of insects) from the Macronesian Islands, Iberian Peninsula and Austral South America.

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