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Structural continuity and multiple alternative stable States in Middle Pleistocene European mammalian communities

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Abstract

Community structure is defined as the distribution and frequency of occurrence of some ecological traits in a set of coexisting species. Many palaeoecological studies of mammal communities assume as valid a model of Community Structure Convergence (CSC), i. e. communities from similar environments should converge to a similar structure. However convincing evidences are known of the existence of multiple Alternative Stable States in ecological communities and similar structures in dissimilar environments have been found. The model of community convergence and the existence of multiple Alternative Stable States are tested here using data from a set of 24 Middle Pleistocene and 50 recent European mammalian communities. Community structure is compared using a multivariate approach. Species are assigned to one of 19 possible ecological groups and a multidimensional "eco-space" is computed based on the abundance of these groups of species in each community, using Principal Components Analysis. The dispersion of the communities in the "eco-space" is used as a measure of their community structure differences. While results indicate the existence of different structures in Glacial and Interglacial northern paleocommunities the considerable intra-group heterogeneity observed contradicts the predictions of the CSC model. The results support the existence of structural continuity (conservation of community structure despite concurrent changes in species composition) in the Iberian and Italian peninsulas during the Middle Pleistocene, as well as a model of cyclic disruption and assembly of paleocommunities with multiple Alternative Stable States in Northern Europe. Northern European assembly processes differed one from the other, giving rise to a community structure more varied than that found in Southern Europe.

Keywords: Community structure; Structural continuity; Multiple Stable States; Mammalia; Pleistocene; Europe

1. Introduction

Basic questions about the mechanisms and processes driving community assembly and determining community structure, and the response of biological communities to environmental change, persist in ecology, although significant theoretical advances towards their answers have been made in recent years (Yachi and Loreau, 1999; Loreau et al., 2003). The definition of Community structure used herein is that given by Brown (1995), as the nonrandom characteristics of locally coexisting species, or the distribution and frequency of occurrence of traits such as body size, foraging habits, time of activity, or reproductive strategies in a set of coexisting species.

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Many studies on mammalian paleoecology aimed at paleoenvironmental reconstruction (Legendre, 1989; Andrews, 1990; Bonis et al., 1992; Ducrocq et al., 1994; Gibernau and Montuire, 1996; Sen et al., 1998; Croft, 2001; Montuire and Marcolini, 2002) apply methodologies based on Community Structure Convergence (CSC), a model of community assembly and evolution developed by ecologists decades ago (Cody and Mooney, 1978; Crowder, 1980; Fuentes, 1980; Losos, 1992). This model takes as given that communities evolved under similar environmental conditions should exhibit similar structures, despite their differing taxonomic compositions. Versions of the model differ in the degree of similarity expected for communities from equivalent environments (Samuels and Drake, 1997), but only the more radical versions are compatible with the methodologies used in mammalian paleoecology. Past environmental conditions may be reliably inferred from the comparison of past and present community structures only if environment determines community structure and, thus, a one-to-one match between environment and community structure exists.

However such a model of Community assembly is far from being universally accepted. Strong empirical (Woodin, 1978; Knowlton, 1992; Drake et al., 1993; Augustine et al., 1998; Schröder et al., 2005) and theoretical (Beisner et al., 2003; Shurin, 2004) evidence of the existence of multiple Alternative Stable States (ASS) in ecological communities has been accumulated in recent years. The existence of multiple ASS in ecology, proposed by Lewontin (1969) years ago, implies that different community structures may come about in localities where similar, or even identical, environmental conditions prevail.

Another challenge to the applicability of the CSC model comes from the observation that, in some cases, moderate to high levels of environmental disturbance do not induce changes in the mammalian species pool (Prothero and Heaton, 1996). In addition, Rodríguez (2004) reported a case of remarkable community structure stability during several Pleistocene climatic cycles in northern Spain (Sierra de Atapuerca). The term "structural continuity" was suggested (Rodríguez, 2004) to designate such a phenomenon, a term first used by Miller (1996) to designate the persistence of regional ecosystems throughout time despite changes in species composition. Structural continuity is defined in the context of community ecology as the persistence of the same (paleo)community structure throughout time, despite concurrent changes in species composition due either to migration or evolution. It is a concept which differs from "coordinated stasis" (Brett et al., 1996), that implies invariance in species composition. Structural continuity may be viewed as a result of resistance, the ability of a community to withstand perturbations without significant change (Tang, 2001) rather than resilience, the ability to return to a previous stable state after disturbance (Beisner et al., 2003).

The European Middle Pleistocene paleontological record provides a fine opportunity to test the CSC model and the existence of multiple ASS in mammalian communities. During this period of about 600 kyr, seven climate cycles of varying intensity occurred (Williams et al., 1988). It has long been recognised that the effects of these climate changes on southern biota was rather different from those on the Central European (Zagwijn, 1992). Temperate- and cold-adapted mammal fauna alternated in Central Europe at every climate cycle (Koenigswald, 1992), but typical "glacial mammals" have been found in the Iberian and Italian peninsulas only in Late Pleistocene sites (Aguirre, 1989; Agustí and Moyà-Solà, 1992; Torre et al., 2001; Palombo and Mussi, 2001). Nevertheless, drastic changes in the Mediterranean vegetation throughout the Pleistocene have been reported (Zagwijn, 1992; Suc et al., 1995). According to the model developed by Costa et al. (1990), Iberian Peninsula "glacial periods" were characterized by the expansion of conifer-dominated steppe formations with pines and other conifers as dominant trees while "interglacial", more humid, periods were dominated by Mediterranean forests. Structural continuity in mammalian paleocommunities occurred at Sierra de Atapuerca in this context of cyclic changes of vegetation (Rodríguez, 2004), and probably of other ecosystem components as well, probably because these environmental changes failed to reach a threshold value.

Two predictions concerning European Pleistocene paleocommunities may be derived from a CSC model:

1) In Central Europe, "glacial" and "interglacial" paleocommunity structure should differ. Since CSC models are based on the premise that community structure is determined by the environmental conditions, communities from different environments should attain different stable states.
2) Central European "interglacial" paleocommunity structure should be similar to that of the southern paleocommunities. In the interglacial stages, southern and Central European environments were probably similar and paleocommunities from similar environments are expected to be similar in structure.

Otherwise, if multiple Alternative Stable States exist, the structure of "interglacial" Central European or British

paleocommunities should be more diverse than that of the Iberian paleocommunities. Central European "interglacial" paleocommunities reassembled every 100 kyr, and their structures were affected by historical processes that varied with each cycle. Thus, different Stable States are expected in every glacial or interglacial stage. In addition, if structural continuity occurred in Southern Europe as proposed by Rodríguez (2004), Mediterranean paleocommunities should be more comparable one with the other and stable over time despite environmental and species composition changes.

These predictions are tested herein using a database of Middle Pleistocene fossil assemblages from various Italian, Spanish, British and Central European sites. According to the CSC model, British and Central European interglacial paleocommunities should be similar and similar, to the Italian and Spanish ones also. Analogously, British and Central European interglacial communities should be similar and different from the interglacial ones.

2. The databases

Faunal lists of 24 Middle Pleistocene Spanish, Italian, British, and Central European paleocommunities were collected from published sources (Table 1 and Fig. 1). Some of the selected sites contribute several stratigraphic levels to the database, corresponding to different time intervals. Only lists with no obvious taphonomic bias where included in the database; i.e. several sites with no or very few micromammal species were excluded from the analysis. The selected lists were checked to maintain taxonomic consistency and tentatively correlated to one Oxygen Isotopic Stage (OIS) based on the curve provided by Williams et al. (1988) using biostratigraphic (van der Made, in press-a,b) and

Table 1
Fossil assemblages considered in the present study

Code		Dating (kyr. BP)	Sedimentary environment	References
Central Europe				
s1	Hummerich A	<200	Loess deposit	Koenigswald and Heintrich, 1996
s2	Schweinskopf	<200	Loess deposit	Koenigswald and Heintrich, 1996
s3	Ariendorf 1	300<>200	Loess deposit Rhine terrace	Koenigswald and Heintrich, 1996; Turner, 1990
s4	Schöningen II	–	Fluvial	Koenigswald and Heintrich, 1996
s5	Heppenloch	–	Karstic	Koenigswald and Heintrich, 1996
s6	Bilzingsleben II	320–412	Fluvial	Koenigswald and Heintrich, 1996; Mania, 1998
s7	Prezletice	–	Fluvial	Koenigswald and Heintrich, 1996
Italian Peninsula				
s8	Isernia La Pineta	–	Fluvial	Peretto, 1996
s9	Grotta Maggiore di San Bernardino	–	Karstic	Bon et al., 1991
s10	Visogliano Loess	–	Karstic (Shelter)	Abazzi et al., 2000
s11	Visogliano Lower levels	–	Karstic (Shelter)	Abazzi et al., 2000
s12	Visogliano Middle–Upper levels	–	Karstic (Shelter)	Abazzi et al., 2000
Iberian Peninsula				
s13	Villacastín	–	Karstic	Arribas, 1994a,b
s14	Cueva de Bolomor Fase I	525,000±125,000	Karstic	Fernández et al., 2000
s15	Atapuerca-Galería GIII	211±32<>256±33	Karstic	Rodríguez, 2004
s16	Atapuerca-Dolina TD8b	602±52	Karstic	Rodríguez, 2004
s17	Atapuerca-Dolina TD10	372±33	Karstic	Rodríguez, 2004
s18	Atapuerca-Galería GII	256±33<>350/317	Karstic	Rodríguez, 2004
Great Britain				
s19	Pontnewydd Cave lower breccia–intermediate complex	>180,000	Karstic	Green et al., 1981
s20	Swanscombe lower loam	–	Fluvial	Ashton et al., 1994
s21	Purfleet greenlands shell bed	–	Fluvial	Schreve et al., 2002
s22	Boxgrove 4b	–	Lagoonal/intertidal	Roberts and Parfitt, 1999
s23	Boxgrove 5a	–	Fen/alder carr pit	Roberts and Parfitt, 1999
s24	Barnham 5c	–	Fluvial	Ashton et al., 1994

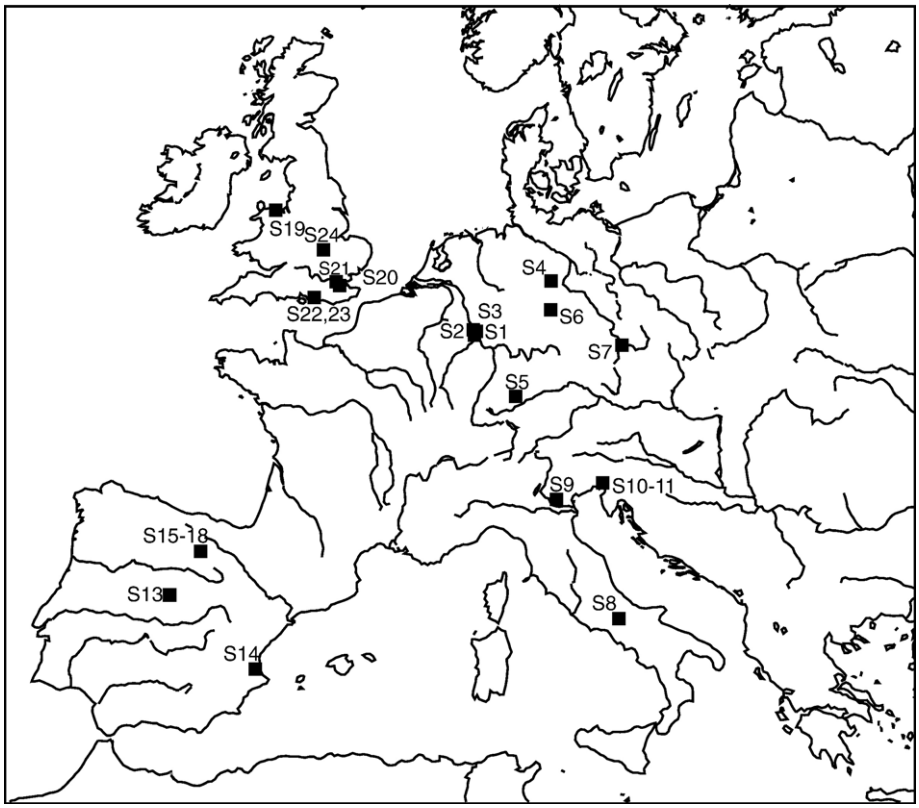

Fig. 1. Location of the 24 fossil assemblages analysed. Codes as in Table 1.

chronological information provided by the original sources (Fig. 2).

In order to evaluate the magnitude of the differences between the Pleistocene paleocommunities, a set of 50 recent Eurasian mammalian communities was collected from published sources (Table 2 and Fig. 3). The area of study was restricted to Eurasia above 35°N, roughly coinciding with the limits of the Palaearctic realm, excluding North Africa. The faunal lists for these localities were selected according to the criteria commented on in

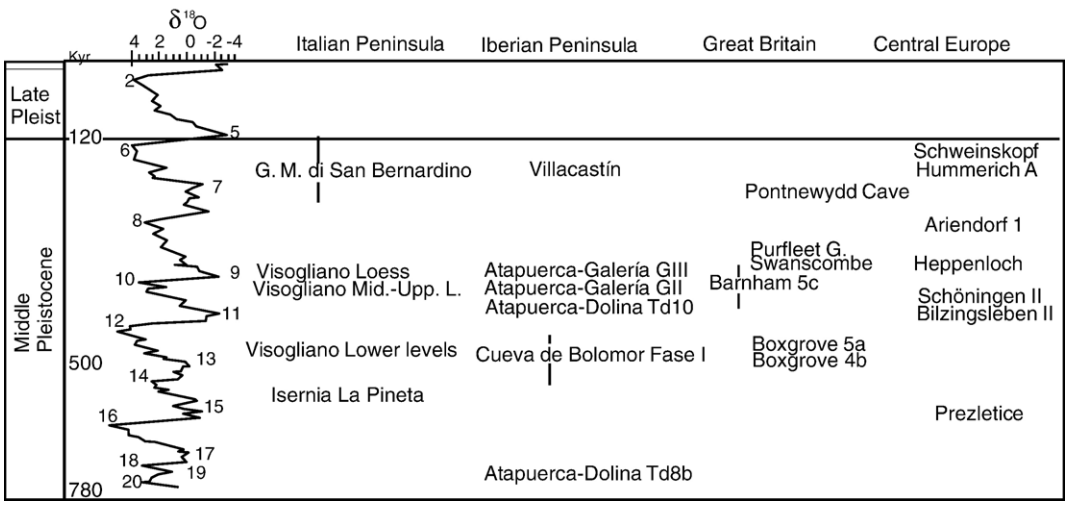

Fig. 2. Fossil assemblage correlation with oxygen isotopic stages (OIS). The OIS curve has been redrawn from Williams et al. (1988).

Table 2
Recent faunas used in the analysis

Cod	Locality	Division	Area (km^2)	Reference
L1	Laplandskiy. (Russian Federation)	Subartic	2784	Rodríguez, 2004
L2	Tsentral'no-sibirskiy (Russian Federation)	Subartic	50,000	Rodríguez, 2004
L3	Darvinsky Zapovednik (Russian Federation)	Subartic	1127	MAB[a]
L4	Pechoro-Ilychskiy (Russian Federation)	Subartic regime mountains	12,537	Rodríguez, 2004
L5	Ubsunurskaya Kotlovina (Russian Federation)	Subartic regime mountains	2843	Rodríguez, 2004
L6	Baikal-Barguzinskiy .(Russian Federation)	Subartic regime mountains	2005	Rodríguez, 2004
L7	Kronotskiyi (Russian Federation)	Subartic regime mountains	11,421	Rodríguez, 2004
L8	Sayano-Shushenskiy Biosphere Reserve (Russian Federation)	Subartic regime mountains	3900	MAB
L9	Pirineos. (Spain)	Humid Temperate	13,000	Rodríguez, 2004
L10	Vosges du Nord. (France)	Humid Temperate	1200	Rodríguez, 2004
L11	Krkonose (Czech Republic)	Humid Temperate	603	Rodríguez, 2004
L12	Hardangervidda, (Norway)	Humid Temperate	3422	Rodríguez, 2004
L13	Torne Lake. (Sweden)	Humid Temperate	965	Rodríguez, 2004
L14	Parc National Suisse (Switzerland)	Humid Temperate	1740	MAB
L15	Urdaibai (Spain)	Humid Temperate	219	MAB
L16	Vessertal Thüringen Forest (Germany)	Humid Temperate	170	MAB
L17	Doñana.(Spain)	Mediterranean	773	Rodríguez, 2004
L18	Cilento and Vallo di Diano (Italy)	Mediterranean	1810	Rodríguez, 2004
L19	Luberon (France)	Mediterranean	1796	MAB
L20	Cazorla. (Spain)	Mediterranean Mountains	1900	Rodríguez, 2004
L21	Cercedilla/Navacerrada. (Spain)	Mediterranean Mountains	131	Rodríguez, 2004
L22	Prespa National Park (Greece)	Mediterranean Mountains	277	MAB
L23	Palava Protected Landscape area. (Czech Republic)	Praire	80	Rodríguez, 2004
L24	Tsentral'no-chernozemny. (Russian Federation)	Praire	48	Rodríguez, 2004
L25	Voronezshkiy (Russian Federation)	Praire	388	Rodríguez, 2004
L26	Tatra Mountains. (Poland)	Praire Regime mountains	1236	Rodríguez, 2004
L27	Aggtelek (Hungary–Czech Republic)	Praire Regime mountains	197	Rodríguez, 2004
L28	Carpathian. (Ukrania)	Praire Regime mountains	578	Rodríguez, 2004
L29	Eastern Beskid or Bieszczadki.(Poland)	Praire Regime mountains	271	Rodríguez, 2004
L30	Kavkazskiy (Russian Federation)	Praire Regime mountains	2957	Rodríguez, 2004
L31	Teberdinskiy Biosphere Reserve (Russian Federation)	Praire Regime mountains	5360	MAB
L32	Bialowieza. (Poland)	Warm continental	1876	Rodríguez, 2004
L33	Berezinsky. (Belarus)	Warm continental	1139	Rodríguez, 2004
L34	Tsentral'no-lesnoy. (Russian Federation)	Warm continental	213	Rodríguez, 2004
L35	Prioksko-Terrasny (Russian Federation)	Warm continental	98	Rodríguez, 2004
L36	Oka River valley (Russian Federation)	Warm continental	772	Rodríguez, 2004
L37	Repetek. Karakum (Turkmenistan)	Temperate desert	346	Rodríguez, 2004
L38	Astrakhanskiy. (Russian Federation)	Temperate desert	668	Rodríguez, 2004
L39	Kazakhstan Steppe (Kazakhstan)	Temperate desert	440,000	Rodríguez, 2004
L40	Amudarya Zapovednik (Turkmenistan)	Temperate desert	485	MAB
L41	Danube Delta. (Romania)	Temperate steppe	5762	Rodríguez, 2004
L42	Srebarna Nature Reserve (Bulgaria)	Temperate steppe	6	Rodríguez, 2004
L43	Great Gobi (Mongolia)	Temperate steppe	53,000	Rodríguez, 2004
L44	Sokhondinskiy Zapovednik (Russian Federation)	Temperate steppe	2110	Rodríguez, 2004
L45	Chernye Zemli Biosphere Reserve (Russian Federation)	Temperate steppe	5329	MAB
L46	Daurskiy Biosphere Reserve (Russian Federation)	Temperate steppe	2277	MAB
L47	Kodry Zapovednik (Moldova)	Temperate steppe	52	MAB
L48	Beinn Eighe (UK)	Marine	48	Rodríguez, 2004
L49	Moor House–Upper Teesdale	Marine	74	Rodríguez, 2004
L50	Schorfheide-chorin (Germany)	Marine	36	Rodríguez, 2004

[a] Man and the Biosphere Fauna Database. UNESCO. Man and the Biosphere Program (MAB). Information Center for the Environment (University of California, Davis)—http://ice.ucdavis.edu.

Rodríguez (2004), so Chiroptera, domestic and exotic species were removed from the lists. While locality area widely differs, sample species richness and area do not correlate (Spearman's $r=-0.0101$, $p=0.94$, $n=50$). Although this lack of correlation may seem unexpected, it confirms other results indicating that on a macro-scale (continent-wide or planetary), environment and history are far more important than area in determining species

richness (Rhode, 1998, Rodríguez et al., 2004). The database of Bailey Ecoregions of the Continents available in the WWF website (http://www.wwwfus.org/ecoregions/) was used to assign every recent locality to one Bailey's Ecological Division (Bailey, 1996) (Table 2 and Fig. 3).

3. Methods

Briefly, the method used to evaluate either recent or fossil community structure similarity, described in detail in Rodríguez (2004), involves the construction of a multidimensional "eco-space" using the absolute frequencies of different ecological groups of species in the communities. The greater the separation of communities in "eco-space", the greater their dissimilarity. In a first step, every species in a community is assigned to one of 19 possible ecological categories (see Table 3 and Rodríguez, 2004 for a detailed explanation). Then, the total number of species in each ecological category is computed for every community or fossil assemblage and a matrix of absolute frequency of ecological types per community or paleocommunity obtained (Tables 4 and 5). This matrix is input to a Principal Components Analysis (PCA) based on a correlation matrix, obtaining a multidimensional eco-space defined by the significant components, i. e. by different combinations of the frequencies (number of species) of ecological types. Although in Rodríguez, 2004 the eco-space was computed using the recent communities only, and the components obtained were used a posterori to calculate the position of fossil assemblages in eco-space, in the present study the entire matrix (including both recent and fossil communities) was input. Finally, the similarity between communities belonging to a particular group is judged by calculating: the Mean Euclidean Distance to the Group Centroid (MEDGC) of those communities; the Maximum Euclidean Distance to the Group Centroid (MXEDGC); and the Mean Weighted Euclidean Distance (MWED) between all the cases of a group. To obtain the value of the MWED index, a matrix of the Euclidean Distances between all cases was computed using, as input data, the scores of the sites and localities in the six significant components, weighted by their corresponding eigenvalue. MWED is computed as the Mean Euclidean Distance between all pairs of cases of a particular group. Weighted Euclidean distances were computed using Clustan Grafics v. 5.0 while PCA was computed using STATISTICA data analysis software system v. 6.

A randomization procedure was used to estimate the probability of obtaining a particular value of MEDGC or MXEDGC for a group of communities selected at random. The test consists of the generation of 1000 random samples of n communities from the observed distribution, i.e. the scores obtained in the PCA, and the computation of the distance measure for each of them. The frequency histogram obtained for the values of the distance measure is used to compute the tail-probability

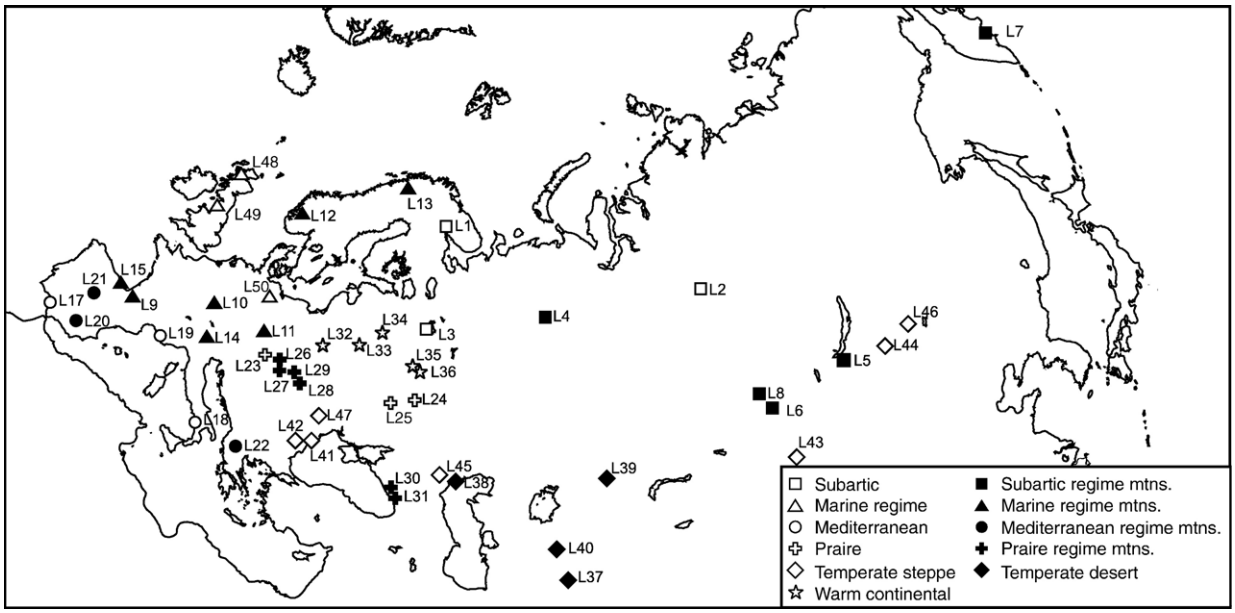

Fig. 3. Distribution of the 50 recent localities included in the analysis. The symbols indicate the Bailey's Ecological Division where the locality is situated. Codes as in Table 2.

Table 3
Ecological categories used to classify fossil and living mammalian species

Code	Name	Definition
v1	Aquatic predator	Preys on aquatic vertebrates and invertebrates.
v2	Small terrestrial predator	Preys on terrestrial vertebrates and birds. Its diet may include invertebrates. Body weight below 30 kg.
v3	Large terrestrial predator	Preys on terrestrial vertebrates, usually mammals. Body weight over 30 kg.
v4	Arboreal predator	Arboreal or semi-arboreal. Preys on tree dwelling vertebrates and invertebrates.
v5	Aquatic predator of invertebrates	Aquatic predator. Feeds only on invertebrate species.
v6	Subterranean predator of invertebrates	Lives underground. Exhibits morphological adaptations to dig galleries. Feeds underground on invertebrate species.
v7	Small terrestrial predator of invertebrates	Terrestrial. Feeds on invertebrates. Body weight below 10 kg
v8	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.
v9	Large terrestrial omnivore	Terrestrial. Feeds on a variety of vegetable food, invertebrates and small vertebrates. Body weight over 1 kg.
v10	Arboreal omnivore	Arboreal. Feeds on seeds, fruit, leaves and invertebrates. Its diet may include small vertebrates and eggs.
v11	Small terrestrial herbivore	Terrestrial. Feeds on plant material. Seeds are usually an important part of the diet. Body weight below 1 kg.
v12	Small sized foregut fermenter	Ruminant. Body weight below 40 Kg. Feeds mainly or exclusively on vegetables.
v13	Medium sized foregut fermenter	Ruminant. Body weight between 40 and 200 kg.
v14	Large sized foregut fermenter	Ruminant. Body weight over 200 kg.
v15	Small sized hindgut fermenter	Non-ruminant. Body weight below 40 kg. Feeds mainly or exclusively on vegetables.
v16	Large sized hindgut fermenter	Non-ruminant. Body weight over 200 kg.
v17	Subterranean herbivore	Lives underground. Exhibits morphological adaptations to dig galleries. Feeds underground on roots, bulbs, etc.
v18	Arboreal herbivore	Arboreal. Feeds on trees and its diet may include leaves, twigs, buds, flowers, fruits and seeds in variable proportions.
v19	Aquatic herbivore	Aquatic adapted for swimming. Feeds mainly on vegetable food.

for a particular value, tabulating the number of times the observed statistic is less than that of the group of communities under consideration. This computation should be done for every n value, since the probability of finding a particular distance value is dependent on the sample size. Recent and fossil communities are tested separately, including only the corresponding subset, because recent and Pleistocene community structures are assumed to be different (Rodríguez, 2001; Rodríguez et al., 2004). As an example, what would the probability be of obtaining a certain value for the mean distance to the centroid taking five Pleistocene paleocommunities at random? If computed using the entire set of recent and paleo-communities, the probability of finding a particular distance value would be underestimated, since data point dispersion would be considerably higher than that of the two subsets considered separately. Consequently a Type I error would be more probable. The rationale underlying this separation is that, given their different structures, it would be impossible for a paleocommunity to plot inside the hypervolume occupied by recent communities, and vice versa. All computations were carried out using a Visual Basic Macro written for Microsoft Excel 97.

In addition, the existence of MWED index median value differences between some groups was tested using the non-parametric Mann–Whitney U test, selected since it is not affected by a MWED value non-normal distribution. (Campbell, 2000).

Four paleocommunity groups were defined according to geographic location: Iberian Peninsula, Italian Peninsula, Great Britain and Central Europe, while recent communities were assigned to one of eleven groups defined by Bailey's Ecological Divisions for Eurasia (Bailey, 1996). In a further step, the Central European paleocommunities were divided into glacial (Hummerich A, Schweinskopf, and Ariendorf 1) or interglacial period subsets (Schöningen II, Heppenloch, Bilzingsleben II and Prezletice). An additional group was composed of all Pleistocene assemblages from karstic deposits, irrespective of their geographic location. This last group was intended to test possible site-type influence on fossil assemblage structure.

4. Results

Table 6 summarizes the results of the PCA that define the "eco-space" in which the recent communities and

Table 4
Absolute frequency of ecological categories (columns) in recent communities (rows)

Code	v1	v2	v3	v4	v5	v6	v7	v8	v9	v10	v11	v12	v13	v14	v15	v16	v17	v18	v19
L1	1	8	1	0	1	0	4	2	2	0	6	0	2	1	1	0	0	1	2
L2	1	8	1	0	1	1	8	3	3	0	7	1	1	1	1	0	0	3	1
L3	2	6	1	0	1	1	5	7	4	0	4	0	1	1	2	0	0	2	3
L4	1	9	1	0	3	0	4	9	3	1	6	0	2	1	2	0	0	1	3
L5	1	11	2	0	1	2	4	5	3	0	20	2	5	1	3	1	1	3	1
L6	1	5	1	0	1	0	7	2	2	0	4	1	3	1	2	0	0	3	1
L7	1	7	2	0	0	0	5	3	1	0	9	0	2	0	2	0	0	1	1
L8	1	9	2	0	1	1	8	3	3	0	10	1	5	1	2	0	0	3	1
L9	1	7	0	1	1	1	6	6	3	1	4	0	3	0	2	0	2	1	1
L10	0	7	0	0	1	1	5	6	2	2	3	0	2	0	1	0	0	1	1
L11	1	9	1	0	2	1	6	7	4	2	4	0	5	1	3	0	1	1	2
L12	0	6	0	0	1	0	2	1	0	0	4	0	2	1	1	0	0	0	2
L13	2	7	1	0	1	1	5	4	3	0	6	0	2	1	1	0	0	3	2
L14	0	5	1	0	2	0	3	4	1	1	4	0	4	0	3	0	0	1	0
L15	1	5	0	1	2	1	5	6	2	1	4	0	1	0	0	0	0	1	1
L16	1	6	1	0	0	2	6	5	2	2	0	0	0	0	2	0	1	0	0
L17	1	6	0	1	0	0	3	5	2	0	1	0	2	0	2	0	1	0	1
L18	1	6	1	0	0	2	6	6	2	1	0	0	0	0	2	0	1	0	0
L19	1	6	1	1	1	1	4	4	2	1	2	0	2	0	2	0	1	1	4
L20	1	5	0	1	0	0	1	3	2	0	1	0	4	0	2	0	1	1	1
L21	1	5	0	0	2	1	5	5	2	0	3	0	1	0	1	0	1	1	1
L22	1	5	2	1	0	0	5	3	1	0	9	0	2	0	2	0	0	1	1
L23	0	7	0	0	1	1	6	6	3	2	3	0	5	0	2	0	1	1	2
L24	1	7	1	0	1	1	4	10	3	1	6	0	2	1	2	0	1	1	1
L25	1	8	1	0	3	0	4	9	3	1	6	0	2	1	2	0	0	1	3
L26	1	7	1	0	2	1	4	1	3	3	0	0	3	0	1	0	0	0	0
L27	1	7	1	0	2	1	5	8	3	1	3	0	2	0	0	0	0	1	1
L28	2	7	1	0	1	1	4	9	3	3	5	0	2	1	1	0	1	1	1
L29	1	8	1	0	2	1	5	7	4	3	3	0	2	2	1	1	1	1	2
L30	2	8	2	0	1	2	9	11	5	2	8	0	4	1	2	0	0	1	1
L31	2	8	2	0	1	2	4	4	5	0	5	0	4	1	1	0	0	1	1
L32	2	8	1	0	0	1	2	3	4	2	1	0	2	2	1	1	0	2	2
L33	1	7	1	0	1	1	4	8	4	1	4	0	2	1	0	0	0	1	3
L34	2	8	1	0	1	1	6	7	4	1	6	0	3	1	2	0	1	2	2
L35	2	6	1	0	2	0	7	9	4	3	4	0	3	2	2	0	0	1	2
L36	2	6	1	0	2	1	6	8	4	3	4	0	4	2	2	0	0	1	3
L37	0	3	1	0	0	0	2	1	1	0	6	2	1	0	2	1	1	0	0
L38	1	5	1	0	1	0	2	4	3	0	3	1	0	1	1	0	0	0	2
L39	0	2	0	0	1	0	4	1	0	0	6	0	0	0	1	0	0	0	1
L40	1	5	1	0	0	0	1	4	2	0	7	0	1	0	1	0	1	0	0
L41	2	9	1	0	2	1	4	7	4	2	4	0	1	1	1	0	2	0	1
L42	1	7	0	0	1	1	5	7	4	3	4	0	2	0	1	0	2	1	1
L43	0	4	1	0	0	1	0	3	1	0	5	2	2	0	2	0	0	0	0
L44	1	12	2	0	1	0	7	4	4	0	11	1	2	1	5	0	1	3	1
L45	0	4	1	0	0	0	2	4	1	0	6	1	0	0	1	0	1	0	1
L46	0	8	1	0	0	0	4	4	3	0	9	1	2	0	2	0	1	1	1
L47	0	7	0	0	1	1	5	6	3	2	3	0	2	0	1	0	2	1	2
L48	1	5	0	0	1	1	2	2	1	0	1	0	2	0	3	0	0	1	0
L49	1	3	0	0	1	1	3	4	1	0	1	0	2	0	2	0	0	1	1
L50	1	7	1	0	2	1	5	7	3	1	4	0	5	1	2	0	1	1	2

See Table 3 for description of categories.

fossil assemblages are compared. Six significant components were retained (Figs. 4 and 5), using Kaiser's criterion, (Hair et al., 1998) that together account for 72% of the variance in the original data (Table 6). The first two components account for 40% of the variance and neatly distinguish recent communities from fossil assemblages, evidence of the existence of major structural differences between them (Fig. 4).

Table 5
Absolute frequency of ecological categories (columns) in fossil assemblages (rows)

	v1	v2	v3	v4	v5	v6	v7	v8	v9	v10	v11	v12	v13	v14	v15	v16	v17	v18	v19
s1	0	0	2	0	0	1	3	1	1	0	2	0	3	1	0	3	0	0	1
s2	0	1	2	0	0	0	0	2	1	0	6	0	2	2	0	4	0	0	1
s3	0	1	0	0	0	1	1	1	2	0	6	0	1	1	0	2	0	0	1
s4	0	1	0	0	1	0	2	2	3	0	5	0	2	1	0	3	0	0	3
s5	0	4	2	0	0	2	2	2	4	0	5	0	3	2	0	3	0	1	2
s6	0	3	2	0	0	1	2	5	4	2	4	1	1	1	0	4	0	1	3
s7	0	3	1	0	2	2	5	4	1	0	8	1	1	0	1	4	0	0	2
s8	0	0	1	0	0	1	2	1	3	0	4	1	2	2	1	3	1	0	1
s9	0	1	1	0	0	1	0	1	2	2	3	2	2	3	1	0	0	0	1
s10	0	1	0	0	0	2	1	1	2	0	3	0	3	2	1	2	0	0	0
s11	0	5	1	0	0	1	1	2	3	1	3	1	3	1	2	1	0	1	1
s12	0	1	0	0	0	1	2	4	2	1	4	1	2	1	1	2	0	0	1
s13	0	3	1	0	0	1	3	3	3	0	4	0	2	0	2	2	0	0	1
s14	0	0	0	0	0	1	3	3	1	1	1	0	3	1	0	3	0	1	1
s15	0	4	2	0	0	0	2	2	1	0	6	0	2	2	3	2	0	0	1
s16	0	1	2	0	1	1	2	3	1	0	4	0	2	2	2	3	0	0	1
s17	0	2	2	0	0	0	0	3	2	0	4	0	3	1	1	2	0	0	1
s18	0	4	0	0	0	0	3	4	2	0	6	0	3	2	4	2	0	0	1
s19	0	1	2	0	0	0	0	1	1	0	4	0	3	1	1	2	0	0	2
s20	0	2	4	0	0	1	0	2	3	0	3	0	3	3	1	4	0	1	2
s21	0	1	1	0	1	0	4	2	1	0	3	0	4	1	0	2	0	1	2
s22	0	4	0	0	0	1	3	3	1	0	5	0	2	1	1	2	0	0	1
s23	0	1	1	0	2	1	3	3	3	1	3	0	2	1	1	2	0	0	1
s24	0	5	0	0	1	1	4	5	1	2	8	0	3	1	2	1	0	0	2

See Table 3 for description of categories.

The first component, accounting for 27% of the original variance, arranges the cases according to their number of small (v1, v2, v7, v8, v9, and v19) versus large species (v3, v14 and v16) (Table 6). Categories including large-sized mammals show high positive loadings in PC2 (v3, v15, v14, v16), although category v11, representing mainly small herbivores (mainly rodents), attains also a high positive loading on this component. On the contrary, subterranean herbivores (v17) and arboreal predators (v4) show moderately high negative loadings. Since most fossil assemblages are rich in large species they have positive scores on this component. The third component accounts for 11% of the original variance and arranges the cases according to their numbers of herbivore species with terrestrial habits and body mass below 40 kg (v11, v12 and v15) versus the numbers of arboreal omnivores (v10) and aquatic herbivores (v19). Although it is tempting to relate such ordination to an environmental gradient, the four Asian and three Balkan communities from the Temperate Steppe Division are subdivided in this component according to their geographical position. Thus, biogeographic factors are also affecting the ordination on PC3. Subterranean mammals (v6 and v17) and small ruminants (v12) have high positive loadings on PC4, while aquatic herbivores (v19) and arboreal predators (v4) have high negative loadings. PC5 classifies the assemblages essentially according to their number of small foregut fermenters (v12) and aquatic predators (v5) versus arboreal predators and medium-sized foregut fermenters (v13). Finally, the more influential categories in the sixth component are small non-ruminant herbivores (v15) and medium sized ruminants (v13), with positive loadings, and arboreal predators and aquatic herbivores with negative loadings.

The main difference between recent and fossil assemblages is the greater large-mammal richness of the later (categories v3, v14 and v16) and a proportionally lower number of small mammals (categories v1, v2, v7, v8, v9, and v19) (Table 6). As shown in Fig. 6, fossil assemblages are probably biased against small mammal species, but their differences from recent communities are not explained just by their low small-mammal richness but also by their high number of large mammals. Similar differences between recent and Pleistocene faunas have been reported in previous studies (Rodríguez, 2001; Rodríguez et al., 2004). Fig. 7 illustrates the relationship between species richness and the scores of the recent and fossil assemblages in PC1. All the fossil assemblages plot above the regression line for the recent ones, and a half of them plot outside the 95% confidence interval for the prediction. Thus, fossil assemblages are not poorer than recent faunas as a whole, although the richest of

Table 6
Results of the PCA of frequencies of ecological categories

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	5,145	2,471	2,239	1,396	1,073	1,013
% Total Variance	27,078	13,005	11,785	7,346	5,648	5,333
Cum. eigenvalue	5,145	7,616	9,855	11,251	12,324	13,337
Cumulative %	27,078	40,083	51,868	59,215	64,863	70,196
Variable	Factor loadings					
v1	−0.791	0.018	0.073	−0.051	0.076	−0.233
v2	−0.877	0.016	−0.279	0.006	−0.038	−0.043
v3	0.034	0.710	−0.146	0.003	0.152	−0.213
v4	−0.090	−0.449	−0.121	−0.314	0.613	−0.329
v5	−0.621	−0.035	0.248	−0.287	−0.371	0.227
v6	−0.208	0.180	0.281	0.671	0.152	−0.035
v7	−0.791	−0.032	−0.095	0.001	−0.106	0.042
v8	−0.792	−0.058	0.270	0.032	−0.103	−0.008
v9	−0.673	0.386	0.292	0.221	0.130	−0.196
v10	−0.526	−0.086	0.535	0.284	−0.028	0.224
v11	−0.184	0.444	−0.632	−0.025	−0.188	−0.091
v12	0.158	0.248	−0.553	0.394	−0.250	−0.146
v13	−0.253	0.413	−0.049	−0.135	0.494	0.566
v14	0.161	0.738	0.313	−0.027	0.089	0.085
v15	−0.357	0.010	−0.586	−0.046	0.160	0.424
v16	0.677	0.453	0.277	0.059	0.111	−0.050
v17	−0.400	−0.392	−0.109	0.381	0.270	−0.150
v18	−0.608	0.370	−0.347	−0.136	0.045	−0.150
v19	−0.261	0.316	0.409	−0.536	−0.070	−0.275

See Table 3 for description of categories.

them is much poorer than many recent communities. However, the poorest assemblage corresponds to a recent community (Kazakhstan Steppe), not to a fossil assemblage. Thus, fossil assemblages have higher scores in PC1 than recent communities of similar richness, and so different structure.

Only in the groups of Prairie Regime Mountains, Warm Continental and Temperate Desert Division recent communities are values for both MEDGC and MXEDGC significant (Table 7), while the three Subarctic Division communities have a significant value for MXEDGC only. However the fact that MEDGC for the Subarctic Division communities is very close to the critical value, suggests that its lack of significance may be due to small sample size (Table 7). It is remarkable that, although their community structure similarity is greater than what could be attributed to chance, the positions of the six Prairie regime Division communities in the "eco-space" separate them in two sub-groups. The four Carpathian localities compose one of these groups and the two Caucasian ones the other (Figs. 3 and 4). Thus, although the structure of these six communities seems to depend on environmental conditions, the influence of purely geographic factors, and the existence of multiple ASS, is also made clear by their positions in the "eco-space". As a matter of fact, the two other groups of communities that exhibit significant community structure similarity correspond to continuous geographic areas. All five Warm Continental Division communities are located in the North-eastern European area of this Division, since the database lack Manchurian localities, the other Eurasian region where this Division is found. Although the Temperate desert Division corresponds to a wide continuous strip through Central Asia (Bailey, 1996) the four localities included in the present analysis are located between the Black Sea and the Himalayans (Fig. 3). Conversely, the groups of communities from the same Division that are not significantly similar in structure are composed of localities thousands of km apart (Fig. 3). The Subarctic Regime Mountains Division sample includes four Asian localities from the Urals, Sayan Mountains and Kamchatka. The eight Marine Regime Mountains Division localities are scattered along a north–south path from northern Scandinavia to the Iberian Peninsula. The three Mediterranean localities are located in Southern France and the Iberian and Italian peninsulas, while the Mediterranean Regime Mountains Division is represented by three Iberian and Balkan localities and the Marine Regime Division by British and Central European localities. Finally, the Temperate Steppe Division is a large, narrow

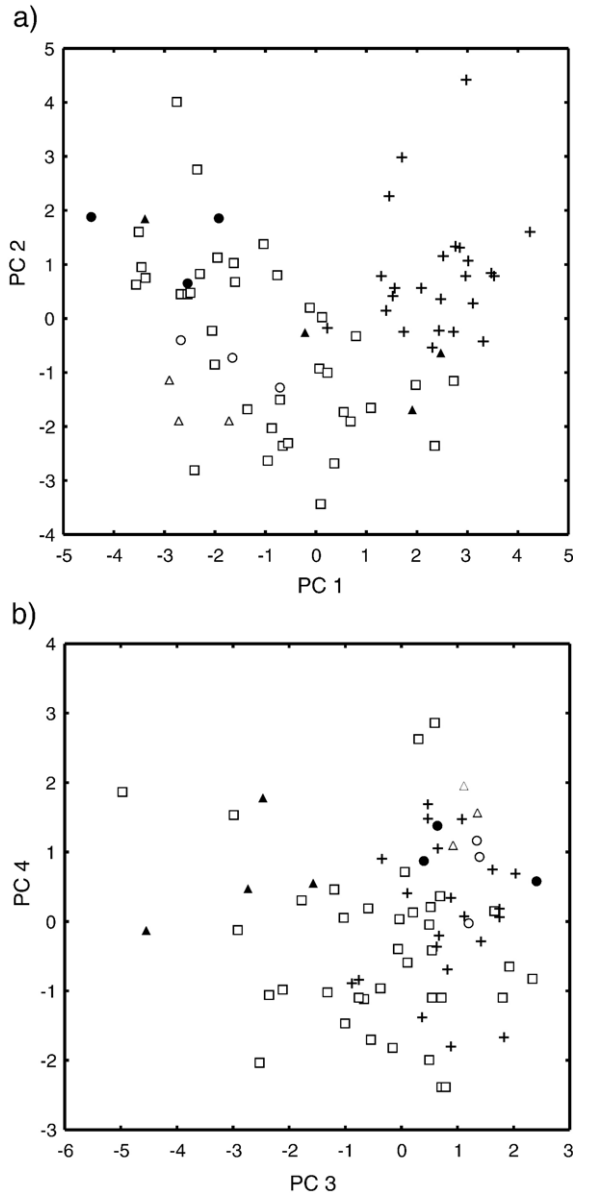

Fig. 4. Scatterplot of Eurasian communities and fossil assemblages in the first four significant Principal Components. Crosses, fossil assemblages; black dots, recent communities from the Prairie Mountain Division in the Caucasus; open circles, recent communities from the Prairie mountain Division in the Carpathians; black triangles, Asian communities from the Temperate steppe Division; open triangles, Balkan communities from the Temperate steppe Division; squares, other recent communities.

strip that runs from the Balkans to Mongolia, represented in the database by 7 localities. A clear separation between the Balkan and Asian localities of this Division may be seen in the first and third components of the PCA (Fig. 4).

To evaluate purely geographic factors influence on community structure, already noted by Rodríguez (2004), three groups were defined, based on geographical proximity, that included localities from different Divisions. One group is made up of Iberian localities, another one by Central European ones, and the last by localities in the Russian plains. All three groups, composed of localities scattered about in areas of less than 1000 km in diameter, exhibit significant similarity in community structure in terms of either the MEDGC or MXEDGC indexes (Table 7).

Regarding the paleocommunities, both the Italian and Iberian groups show significant community structure similarity (Table 7) in terms of either the MEDGC or MXEDGC indexes. In addition, there are not significant MWED value differences between these two groups (Table 8). Moreover, similarity in structure in the group composed of all Italian and Iberian assemblages together is also significant (Table 7), although they seem to be subdivided in PC4 according to peninsula of origin (Fig. 8). As a mater of fact, the Italian assemblages appear as distinct in PC4. Conversely, the British and Central European assemblage values for both the MEDGC and MXEDGC similarity indexes are high and non-significant. Although the two subsets of Central European paleocommunities seem to occupy two different areas in PC1 (Fig. 8) none of their similarity index values are significant (Table 7). Certainly, the values for both indexes for the three "glacial" paleocommunities are the lowest value for both indices, but it should be

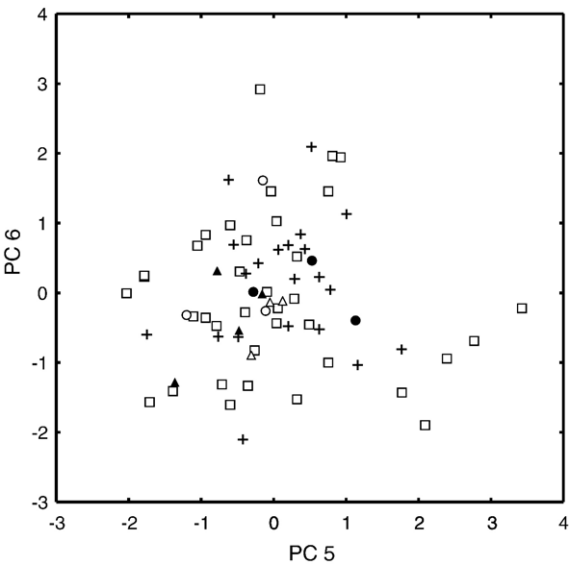

Fig. 5. Scatterplot of Eurasian communities and fossil assemblages in Principal Components 5 and 6. Symbols as in Fig. 4.

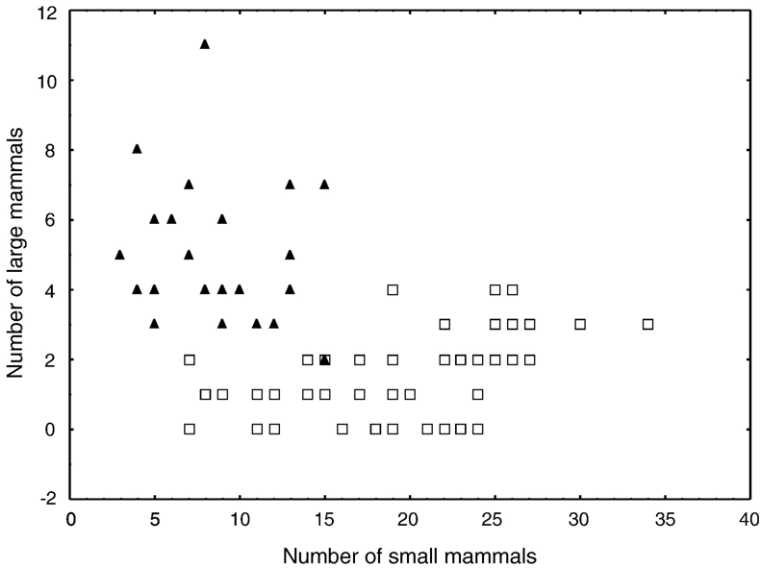

Fig. 6. Number of small (v1, v2, v7, v8, v18) versus large mammals (v3, v14, and v16) in recent communities (squares) and fossil assemblages (triangles).

remembered that the probability of finding a particular value for these indexes is dependent on the sample (group) size. Comparison of the MWED values for the Iberian, Italian, Central European and British paleocommunities shows that the values for this index are lower in the southern paleocommunities than in the northern ones, evidence of a high degree of paleocommunity structure similarity in southern Europe.

In order to test the possible influence of taphonomic processes on the structure of fossil assemblages, a group was composed of all the assemblages from karstic sites. The MEDGC of this group is significantly lower than the expected value for cases selected at random (Table 7). However, the MXEDGC value is remarkably high and non-significant.

5. Discussions

5.1. Multiple stable states in recent communities

In seven out of the 11 cases considered, recent communities belonging to the same ecological Division are not significantly similar. This result confirms previous observations (Rodríguez, 2004) made while using a slightly different ecological community classification and is evidence of the existence of MSS in mammalian communities (see also Rodríguez et al., 2006). The Divisions that render non-significant results are those represented by localities widely scattered over large areas, larger than a million square kilometers roughly. In some of those Divisions, subsets of localities seem to cluster according to geographical position. Finally, localities classified in different but proximate Divisions are significantly similar in community structure. This result

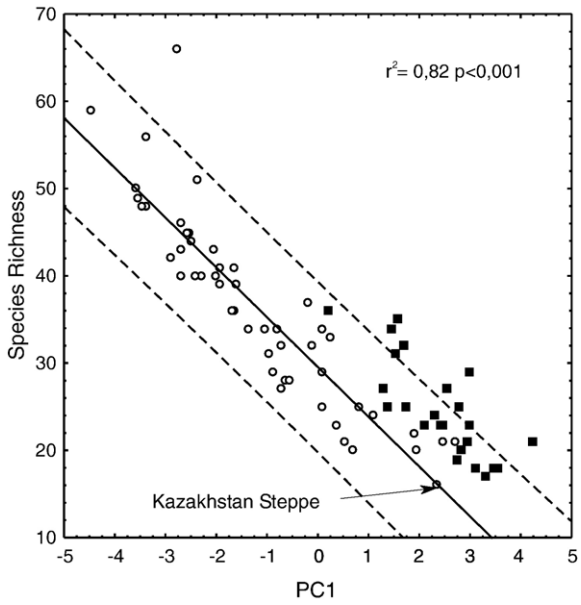

Fig. 7. Plot of species richness versus the scores of recent and fossil assemblages on PC1. The regression line for recent communities and 95% confidence interval lines are shown. Note that all fossil assemblages plot above the regression line and most of them are outside the 95% confidence interval. Black squares: fossil assemblages; open circles: recent assemblages.

Table 7
Distance measures for the different groups of cases considered in the present study

Middle Pleistocene assemblages	MEDGC	p	MXEDGC	p	MW ED	N cases
Central Europe	2.14	0.645	2.62	0.213	0.38	7
Italian peninsula	1.30*	0.010	1.60*	0.010	0.24	5
Iberian peninsula	1.46*	0.024	1.97*	0.023	0.26	6
Great Britain	2.24	0.781	4.26	0.999	0.42	6
Glacial Central Europe	1.18	0.128	1.44	0.129	0.33	3
Interglacial Central Europe	2.13	0.940	2.41	0.750	0.33	4
Iberian and Italian sites	1.65**	0.005	2.52*	0.026	0.26	11
Karstic sites	1.82*	0.047	3.23	0.285	0.27	12
Recent communities						
Subartic	1.71	0.051	1.78*	0.016	0.37	3
Subartic regime mountains	2.83	0.333	4.49	0.661	0.54	5
Marine regime mountains	3.11	0.395	3.65	0.055	0.54	8
Mediterranean	2.51	0.346	3.24	0.426	0.43	3
Mediterranean regime mountains	2.54	0.367	3.19	0.394	0.42	3
Praire	1.99	0.112	2.56	0.158	0.30	3
Praire regime mountains	2.00**	0.003	2.82**	0.005	0.39	6
Warm continental	1.85**	0.002	2.06**	0.001	0.34	5
Temperate desert	2.02*	0.023	2.54	0.023	0.38	4
Temperate steppe	3.32	0.672	5.14	0.770	0.67	7
Marine regime	1.94	0.104	2.77	0.223	0.45	3
Iberian	2.21*	0.030	2.94*	0.042	0.36	5
Central Europe	1.81**	0.009	2.29*	0.010	0.35	4
Russian planes	1.79**	0.009	2.47*	0.020	0.31	4

The probabilities (p) for the mean (MEDGC) and maximum (MXEDGC) Euclidean distances estimated from the randomization test are indicated. Asterisks mark significant values at the 0.05 and 0.01 probability level.

provides evidence of the influence of biogeographic factors, that in some cases may be even more influential than environmental factors, in the assemblage process of ecological communities. The importance of biogeographic, or historic, factors in the composition of communities has been stressed by many authors, (Ricklefs and Schluter, 1993; Brändle et al., 2003; Chase, 2003; Ricklefs, 2004). The gathering of species from different regional pools in localities far apart determine the existence of differences in their respective community structures. Thus, although the environments are similar, the nature of their regional pool constrains the possible stable states for each locality.

It may be argued that non-significant similarity in some groups of communities is the consequence of an inadequate level of analysis, since Divisions are very large units. Bailey's categories of lower rank (Provinces) would provide an alternative way to classify recent communities. Certainly, some of the non-significant groups include localities from several different Provinces of the same Division. In Bailey's classification, Divisions are defined on the basis of purely climatic criteria, while Provinces are further subdivisions based on the climax plant formation that geographically dominates the area (Bailey and Hogg, 1986). Provinces may implicitly, although unintentionally, incorporate some biogeographic factors in their definition, and so a greater degree of similarity is expected between communities from the same Province than from the same Division. However, the structural similarity of geographically close communities from different Divisions (and then from different Provinces), would not be affected if Provinces were used instead of Divisions. Thus, the relevance in some cases, of biogeographic as opposed to

Table 8
Mann–Whitney U test for differences in the median value of the weighted Euclidean distance between paleocommunities from the same region

	UK(21)	IB(15)	IT(15)
CE (21)	$U=143$ $p=0.6417$	$U=59$ $p=0.0016$	$U=35$ $p=0.0031$
UK (21)		$U=46$ $p=0.0058$	$U=23$ $p=0.0039$
IB (15)			$U=63$ $p=0.4881$

The number of distances between pairs of paleocommunities from the same group (sample size) is indicated inside the parentheses. CE: Central Europe; UK: Great Britain; IB: Iberian Peninsula and IT: Italian Peninsula.

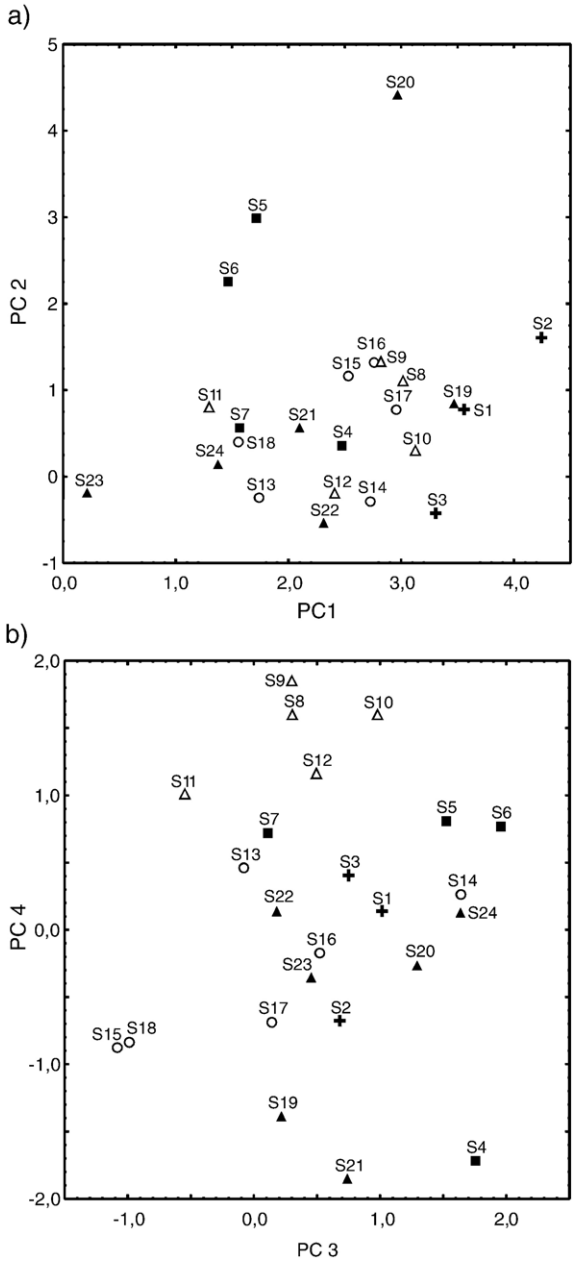

Fig. 8. Scatterplot of paleocommunities in the first four significant components. PC1 divides the Central European Middle Pleistocene assemblages into an interglacial (black squares) and a glacial subset (crosses), while PC4 seems to separate Iberian (open circles) from Italian (open triangles) paleocommunities. Black triangles represent British paleocommunities. Codes as in Table 1.

environmental factors would not be lessened by a scale change in the analysis.

The present results also suggest that communities from localities environmentally different but spatially close are significantly similar. Assembly from the same regional species pool, drives community convergence to the same Stable State. This explains the significant similarity of the Iberian, Central European and Russian Plains groups of localities (Table 7). Put in other way, the same Stable State may exist under different environmental conditions. Thus, paleocommunity structure similarity throughout time would not necessarily involve equivalent environmental conditions and Structural Continuity does not imply absence of disturbances, but only that environmental differences did not exceed the resistance threshold of the paleocommunities.

5.2. Structural continuity in the Middle Pleistocene

The results presented herein support the Structural Continuity hypothesis for the Italian and Iberian peninsulas, where community structure was found to be very similar, regardless of paleocommunity age or location. Both peninsulas are now environmentally heterogeneous, and it may be assumed that a similar degree of heterogeneity existed in the past (Suc et al., 1995). During any given period, communities with slight variations in composition inhabited various locations under a variety of environmental conditions. Their structure underwent little or no change over time, so paleocommunity structure from a variety of periods and sites from the same peninsula turned out to be very similar. Most remarkably, this paleocommunity structure stability lasted at least 600 kyr, and probably longer (Rodríguez, 2004), and occurred during a period of environmental instability. This interpretation is supported by palynological analyses that indicate different environments for Visogliano (Abazzi et al., 2000) and Isernia La Pineta (Accorsi et al., 1996) and remarkable environmental variation for the Atapuerca sequence (Garcıa-Antón, 1989). This pattern implies that perturbation did not reach a threshold value in southern Europe during the Middle Pleistocene. In other words, climatic cycles induced changes of relatively low amplitude in southern Europe, as has been long recognised (Zagwijn, 1992; Suc et al., 1995).

Significant Italian and Iberian (all eleven paleocommunities) structure similarity would seem to have come about despite the two peninsulas' relative isolation, one from the other. However, spatially related differences existed between them, as evidenced by their position in PC4. This similarity might only be the result of either the persistence of an ancestral community structure common to both peninsulas and northern Europe or to a phenomenon of ecological convergence (Cody and Mooney, 1978; Samuels and Drake, 1997; Ben-Moshe et al.,

2001). Evidence to support one cause or the other is lacking at present.

5.3. Possible effects of taphonomic biases

Since fossil assemblages are neither random samples nor complete inventories of paleocommunities, taphonomic processes operating on fossil assemblage genesis may influence the observed paleocommunity structure patterns of similarity and dissimilarity. While knowledge of all the taphonomic factors that took part in the formation of these assemblages is unattainable, arguments based on available information may still be put forward. Site characteristics must be considered, since all Iberian and four out of five Italian assemblages were recovered in karstic sites. Community structure in the group of 12 assemblages from karstic sites, including one Central European and one British assemblage, show significant similarity in community structure as measured by the MEDGC index. This may be a consequence of the considerable influence of the 10 southern European localities on this index. Conversely, the MXEDGC index value, considering the most distant case only (Heppenloch), is non-significant for this group. Moreover, the single Italian non-kastic site (Isernia La Pineta) assemblage community structure is very similar to that of the other four Italian assemblages. In the light of the available evidence, it thus would seem unlikely that karstic-site origin was the cause of the similarities observed in southern assemblages.

Certainly, other taphonomic factors such as accumulation agents, transport, etc may have biased the structure of these 24 fossil assemblages. As a matter of fact, many fossil assemblages seem to be biased against small mammals in comparison with recent communities. However, the key question here is not whether these assemblages are absolutely unbiased samples of the paleocommunities but rather if the observed patterns may have been caused by taphonomic processes. As argued in other studies (Bennington and Bambach, 1996; Rodríguez et al., 2004) it is hard to believe that dissimilar processes operating on dissimilar paleocommunities have created the pattern of similarity observed in southern paleocommunities. Certainly, evidence of dissimilar processes includes TD10 level of Gran Dolina at Atapuerca, a campsite; TD8 probably a hyena den: GII and GIII natural pit-fall traps (Dıez et al., 1999; Rosell, 2001); Isernia la Pineta, considered to be largely the result of human activities (Accorsi et al., 1996); Cueva de Bolomor Phase I, humans and carnivores accumulations agents (Fernández et al., 2000). Conversely, concerning the Central European and British assemblages, it could be argued that the observed structure dissimilarities are just a consequence of various taphonomic processes operating on similar paleocommunities, certainly an objection very difficult to rule out. Nevertheless, accepting it would require an explanation of why these processes created differently biased assemblages only in Great Britain and Central Europe, but not in southern Europe. This possibility would involve taphonomic processes different in Northern and Southern Europe, and evidence of such differences is lacking. In summary, with the available evidence, the most parsimonious explanation of the observed pattern seems to be that observed fossil assemblage similarities and differences are reflections of actual differences in the structure of the paleocommunities they represent.

5.4. Multiple alternative stable states and community structure in the Middle Pleistocene

The Community Structure Convergence model predicts that Central European glacial and interglacial paleocommunities should be different and that northern and southern interglacial communities should be similar. Results are congruent with the first prediction (Fig. 8). This is a remarkable result since similar analyses with recent communities have found that such differences exist only between localities from remarkably different environments (Rodríguez, 2001; Rodríguez et al., 2006).

The second prediction of CSC model is derived from the assumption that there is a single correspondence between environment and community structure and that some of the selected Northern European and Southern paleocommunities inhabited similar environments. Such southern and northern paleocommunity structure similarity, if observed, could only be the result of a process of convergence. The results do not support this prediction, since none of the Central European or British interglacial paleocommunities plots inside southern paleocommunity hypervolume. There are two possible explanations for this lack of similarity: a) there are no northern paleocommunities from environments similar to those of the southern ones in the database; or b) some of the British and/or Central European paleocommunities inhabited environments similar to the environments of some Mediterranean paleocommunities, but their structures were different. Only the second explanation is in contradiction with the prediction, while evidence to support one explanation or the other is lacking.

On the other hand, results are in agreement with the existence of multiple ASS in northern Europe and Structural Continuity in Southern Europe. Non-significant

similarity indices suggest that glacial, or interglacial, northern paleocommunities did not converge to a single Stable State, but to different states in each climate cycle. Northern paleocommunities re-assembled in each climate cycle following a different path that led them to different states of equilibrium. On the contrary, the significant similarity for the Iberian and Italian localities supports the Structural Continuity hypothesis. Structural Continuity implies community taxonomic composition changes without significant community structure changes. In the case of the Atapuerca paleocommunities a moderate turnover was detected around 500 ka BP that did not change community structure (Rodríguez, 2004). No major turnover pulses are detected in continental Europe during the Middle Pleistocene (Azanza et al., 2000), although immigration of Asian taxa and local evolution of some lineages occurred throughout the period (van der Made, in press-a) and a moderate replacement is detected from the Cromer to the Hoxnian in Great Britain (Stuart, 1982).

With all these results in mind an explanation of the processes driving mammalian community structure in Middle Pleistocene Europe may be attempted using the ball-in-cup analogy outlined in Fig. 9 and proposed by Beisner et al. (2003). All the possible states of the system (community structures) are represented by the surface of the figure, or landscape, while the actual community structure is represented by the position of the ball resting on the surface (Beisner et al., 2003). In absence of perturbations the ball is always in the bottom of a "valley", and it returns to this position after a disturbance, unless the disturbance is large enough to roll the ball over the "mountain" to another "valley". The shape of the landscape, position of the "valleys" and height of the "mountains", are determined by the environment, glacial and interglacial environments determine different landscapes, with different Stable States (valleys). In northern Europe, the glacial cycles determine large changes in the landscape. Thus, a community that is situated in a stable state during an interglacial period (Fig. 9a) is moved to another state when the system changes to glacial conditions (Fig. 9b). In the next cycle, the system returns to an interglacial configuration, but the community has been driven to a Stable State different from the previous interglacial one (Fig. 9c). Similarly, a new change to glacial conditions moves the community to a new Stable State (Fig. 9d). On the contrary, southern paleocommunities were not driven from one state to another by climate cycles, since their impact was less intense (Fig. 9e–h) and did not modify the positions of the Stable States.

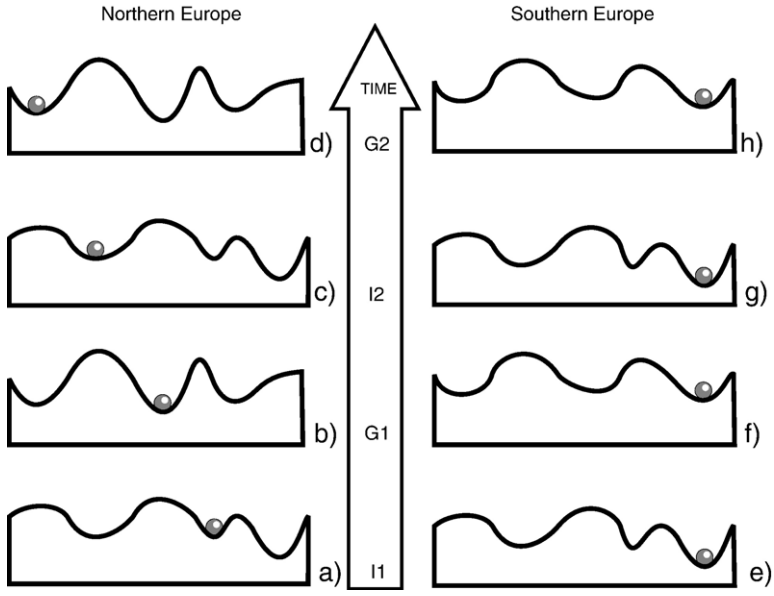

Fig. 9. Model of the changes in Community structure in relation to climatic cycles in Middle Pleistocene Europe using ball-in-cup diagrams and the conceptual framework developed by Beisner et al. (2003). The surface, or landscape, determines the position and characteristics of all the stable states for a particular environment, while the ball resting on the surface represents the actual community structure. Glacial (G1, G2) and interglacial (I1, I2) environments determine different landscapes, with different stable states. In northern Europe (left part of the figure) glacial cycles determine large changes in the landscape, that move the community from one state to another. Return to the previous environmental conditions does not necessarily imply recovery of the previous stable state. In southern Europe environmental changes were less intense and the modifications induced in the landscape did not change the positions of the stable states (right part of the figure).

6. Conclusions

Italian and Iberian peninsula mammalian paleocommunity structure remained significantly similar throughout the Middle Pleistocene, a phenomenon named Structural Continuity by Rodríguez (2004). Conversely, Central European and British paleocommunity structure was much more heterogeneous throughout this period, showing no evidence of structural continuity, but rather indicate the existence of multiple Alternative Stable States for the glacial and interglacial communities. These results are in contradiction with the most radical versions of the Community Structure Convergence models, in particular with the existence of a one-to-one correspondence between community structure and environment. A call for caution is in need when paleoenvironmental reconstructions based on the assumption of community convergence are attempted.

A model of community evolution for Pleistocene Europe may be established as follows: Mediterranean paleocommunities experienced moderate environmental disturbance (Costa et al., 1990; Zagwijn, 1992) that was not disruptive, so a high degree of community structure similarity can be observed over time. Whereas in Central and Northern Europe disturbance was considerably more disruptive, the regional species pool changed, and paleocommunities there were disrupted and disengaged after each climate cycle. The glacial or interglacial paleocommunities reassembled roughly every 100,000 years, giving rise to more heterogeneous community structures, representing different Alternative Stable States.

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