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Ecological patterns in the trophic-size structure of large mammal communities: a 'taxon-free' characterization

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ABSTRACT

Questions: Are different types of terrestrial mammalian-dominated ecosystems characterized by specific taxon-free patterns in the trophic structure of the mammalian community? If so, are these patterns an intrinsic property of the ecosystems? If this is indeed true, the trophic structure of present-day mammalian communities can be used for the synecological reconstruction of past terrestrial mammalian-dominated communities.

Data: 110 Recent large mammal communities, 86 from Africa and 24 from Asia, and one large mammal assemblage from the early Pleistocene locality at Venta Micena (Guadix-Baza Basin, southeast Spain).

Search method: Stepwise discriminant analysis generated mathematical algorithms that characterize definite patterns in the trophic structure of the mammalian communities from each type of ecosystem. Algorithms adjusted with African communities were applied to the Asian and Pleistocene ones, whose species are completely different from those of Africa, to test if these patterns are independent of specific historical circumstances and taxonomic composition.

Conclusions: Terrestrial mammalian-dominated ecosystems are characterized by definite taxon-free patterns in the trophic structure of the mammalian community. These patterns are an intrinsic property of the ecosystems, independent of their specific historical circumstances and taxonomic composition. Therefore, the trophic structure of present-day mammalian communities can be used for the synecological reconstruction of past ones. The sedimentologic and taphonomic information for the early Pleistocene community of Venta Micena is indicative of a wooded savanna; this type of ecosystem is also indicated by the trophic structure of the mammalian community. This congruence supports the hypothesis that the ecological patterns identified here are an intrinsic property of past ecosystems, at least as far as Pleistocene land mammal-dominated communities are concerned.

Keywords: complex patterns, discriminant analysis, evolutionary paleoecology, mammal communities, paleosynecological reconstruction, taxon-free characterization, trophic structure, Venta Micena.

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INTRODUCTION AND BACKGROUND

Paleoecological analyses include the inferences of past ecological associations (paleosynecology) and those related to the life styles and preferred habitat of the individual species (paleoautecology). From this perspective, evolutionary paleoecology studies the physical and biotic context of fossil organisms, as well as the consequences of the changes in such context on the evolution of extinct lineages. The four main objectives of this comparative approach (Damuth, 1992; Wing *et al.*, 1992) are: (1) to evaluate whether ecological concepts defined in modern communities are valid for studying the structural properties and changes over time and across space in the composition of paleocommunities; (2) to determine which types of ecological properties and interactions are independent of the taxonomic composition and the time period studied (i.e. the 'taxon-free' approach to the characterization of communities); (3) to study long-term responses of paleoecosystems to changing physical and biotic conditions; and (4) to elucidate the influence of ecological relationships on the long-term evolutionary history of lineages.

Once the preservational completeness of the fossil assemblage (i.e. its fidelity with respect to the original community) has been estimated using taphonomic analysis (e.g. Damuth, 1982; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001), it is then necessary to infer the autecological properties of those species preserved in the assemblage before the synecological analysis at the community level (see review in Palmqvist *et al.*, 2003). The autecology of extinct species may be reconstructed using three basic methods (Wing *et al.*, 1992; Palmqvist *et al.*, 2003): (1) based on functional analysis of their morphology (which is facilitated if they are closely related with extant species) for obtaining biomechanical and ecomorphological inferences; (2) based on biogeochemical techniques (e.g. trace-element analysis and stable-isotope ratios) for reconstructing dietary niches, habitat preferences and paleotemperatures; and (3) based on the sedimentary context and taphonomic attributes of fossils as well as on their distribution across facies.

Although the reconstruction of the autecological adaptations of those more common species that inhabited past communities is the procedure most commonly used in paleo-synecological analysis, an alternative approach may be based on the use of biologically meaningful properties of the whole community, such as species richness or the distribution of species among feeding categories and body size classes (e.g. Andrews *et al.*, 1979). However, the adequacy of these properties for ecological characterization must be tested with modern communities before paleoecological analysis, because such properties will be appropriate only if they are independent of the historical circumstances and taxonomic composition of communities [i.e. the 'taxon-free' approach (Damuth, 1992)].

Clearly, the easiest way for comparing the composition of modern and past communities is to use their faunal lists, although this method is obviously of limited use in the case of those fossil assemblages that include species without close living relatives. In addition, faunal lists do not provide information on the role of species within the paleocommunity or on their ecological interactions. Due to such limitations, most researchers have followed ecomorphological and biogeochemical approaches for inferring the autecological properties of extinct taxa (see review in Palmqvist *et al.*, 2003). Once this is achieved, the species are placed within ecological categories [e.g. size classes or locomotor and trophic types (Damuth and MacFadden, 1990; Janis, 1995; Kappelman *et al.*, 1997; Lewis, 1997; Spencer, 1997)] and the relative frequencies of such categories in the paleocommunity are compared with those seen in modern ecosystems (Andrews *et al.*, 1979; Damuth, 1992; Reed, 1997, 1998; Van Valkenburgh, 1985, 1988, 1989, 1991). For example, Fig. 1
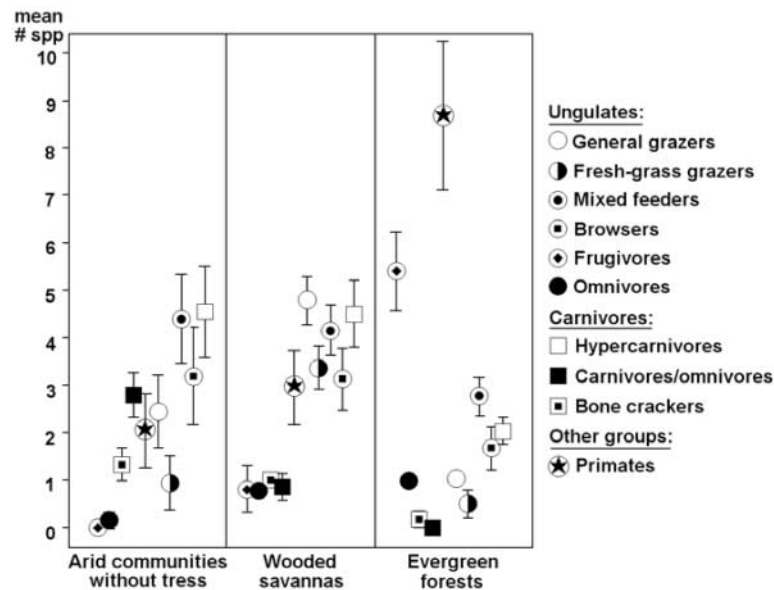
Fig. 1. Mean number of species distributed among ecological categories based on feeding behaviour in African large mammal communities inhabiting the three major ecosystem types.

shows the mean number of large mammal species grouped according to their feeding behaviour in those African communities that inhabit the three major vegetational types: evergreen forests, wooded savannas and bushlands, and treeless arid communities with sparse vegetational cover. It is evident from this figure that the abundance of primate species, and of frugivorous species among ungulates, increases from arid environments to forested ones. In addition, grazing and mixed feeding ungulates are more diverse in wooded savannas and bushland. Finally, the number of hypercarnivore and bone-cracking species is inversely correlated with tree coverage in the habitat.

The aim of this paper is to determine whether the trophic and size structure of a large mammal community is a biologically meaningful property that characterizes each ecosystem type. In doing so, we will search for ecological patterns in the trophic and size structure of a large set of modern mammalian communities from Africa. These patterns are identified by means of mathematical algorithms derived from canonical discriminant analysis, based on the number of large mammal species from different trophic categories subdivided into body size groups. The algorithms obtained are then applied to modern communities from Asia, whose species, and the historical circumstances under which they evolved, are completely different from those in Africa. This allows us to establish whether the patterns identified in the structure of mammalian communities emerge as an intrinsic property of the ecosystems, or are merely the consequence of a similar taxonomic composition among African communities that share similar ecological features and are not separated by important biogeographic barriers.

Finally, we apply these algorithms to the early Pleistocene large mammal assemblage from Venta Micena (Guadix-Baza Basin, southeast Spain), a locality currently interpreted as a hyena den with a high compositional fidelity to the original mammalian community

(Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). This allows us to test if the ecological patterns identified here are maintained through time, at least as far as Pleistocene land mammal-dominated ecosystems are concerned.

PALEOSYNECOLOGICAL ANALYSIS OF LARGE MAMMAL COMMUNITIES

Cenograms are an easy and direct approach for estimating the distribution of vertebrate species among size classes in a community (Valverde, 1964). Cenograms rank species in decreasing order by body size relative to the logarithm of their body mass. The slope of the resulting graph can be related to the amount of tree cover and rainfall in the environment inhabited by the community, which has allowed the synecological reconstruction of several extinct communities (e.g. Fleming, 1973; Legendre, 1986; Montuire, 1999). These diagrams, however, merely reflect differences based on the number of species and their range of body mass, and are thus of limited use in paleoecology (Andrews, 1996; Rodríguez, 1999).

Inferences derived from the trophic structure of mammalian communities have also been used in paleosynecological reconstructions. Several researchers have found that the relative frequencies of species classified among trophic groups allow the characterization of major ecosystem types (see review in Damuth, 1992), and that the relationship between the number of predator and prey species is also a diagnostic feature (Arnold, 1972; Fleming, 1973; Cohen, 1977; Cole, 1980). For example, Andrews *et al.* (1979) represented the trophic structure of terrestrial communities of large mammals as histograms of relative abundance of species per feeding group (as well as other ecological categories such as the distribution of species among size classes and types of locomotion), and then compared the shape of these histograms between modern and extinct communities, in order to infer the ecological properties of the latter ones.

These paleoecological analyses allow the use of multivariate approaches, which provide a more robust ecological characterization. Reed (1997, 1998) was a pioneer in the application of multivariate statistics to the synecological reconstruction of extinct mammalian communities. She classified 30 modern sub-Saharan large mammal (>500 g) communities among six major vegetational categories (forest, closed and open woodland, bushland, shrubland, and grassland) (see details in Reed, 1997). Reed (1997) used two sets of variables: (1) the number of species belonging to different taxonomic categories (taxonomic variables); and (2) the number of species with different feeding preferences, such as the number of grazers, browsers, and so on, and modes of locomotion (ecological variables). Reed (1998) used both univariate and bivariate analysis to estimate which ecological variables are more correlated with vegetational habitat. For example, the percentage of frugivorous species correlates directly with the extent of tree coverage in the habitat, and the relative abundance of species with terrestrial locomotion correlates inversely with tree coverage (Reed, 1997: figures 5–7). The ecological variables that correlated strongly with vegetational gradients were subsequently used for the paleosynecological characterization of two Pliocene assemblages from Makapansgat. She also performed a discriminant analysis to assess the potential of either taxonomic or ecological variables to classify modern and extinct communities according to major vegetational types (Reed, 1998). The discriminant functions obtained using both sets of variables correctly reclassified 100% of modern communities among major vegetational types, but when they were applied to the extinct assemblages the results were not coherent. Specifically, the discriminant functions based on the taxonomic composition placed both fossil assemblages very distant from all multivariate means or group centroids,

which implies that community structure based on the relative abundance of taxa did not provide a robust determination. The ecological discrimination, based in part on the trophic structure of modern mammalian communities, also placed both extinct communities more distant from all group centroids than any sample used in the adjustment of the discriminant functions, although the assignments obtained could have a certain predictive value in this case. However, the predictions of the discriminant functions for the Makapansgat assemblages differed from those derived from univariate and bivariate analyses.

Reed (1998) concluded that both univariate and bivariate analyses indicate that the Makapansgat fossil assemblages were accumulated in a bushland environment, probably with edaphic grasslands and riverside trees. These results agreed well with those obtained from paleoecological reconstructions based on pollen content and sedimentological studies (reviewed in Reed, 1998). She also concluded that the discriminant analyses based on the taxonomic and ecological variables did not classify the paleocommunities consistently because their community structure was different from that of modern ones. It is evident that the taxonomic structure of the Makapansgat assemblages was quite different, containing the taxa Chalicotheriidae, Boselaphini, Ovibovini, Gomphotheriidae and Machairodontinae, that are either extinct or extirpated from Africa. Reed (1998) was thus unable to include these taxa in her analyses. While it is to be expected that the taxonomic structure of mammalian communities should change throughout time or space, it is not so clear if this would also be expected of the ecological community structure.

There are some methodological problems that could justify these results. For example, the ecological assignation of each extinct species to one of the 12 trophic categories used by Reed (1998) may not be fully reliable. Using craniodental data, Janis (1995) was able to correctly discriminate only 93 of 127 (73%) ungulate species distributed among the three general feeding types (i.e. browsers, mixed feeders and grazers). Using a similar set of morphological variables, Reed (1998) attempted to discriminate among six feeding categories for herbivores. In addition, a serious limitation of her analyses derives from the ratio between the samples analysed and the number of variables used to elaborate the discriminant functions. Specifically, there are on average only five samples within each major vegetational category in Reed's data base, but the number of taxonomic and ecological variables (23 and 17, respectively) is very high (see details in Reed, 1998). Although this biased ratio allows a high percentage of correct reclassifications to be obtained for those samples used in the adjustment of the discriminant functions, such functions are probably based on the particular features of the samples compared, rather than on those general properties characterizing the broader spectrum of all herbivore species in each category. For these reasons, the discriminant functions have little predictive power with new samples, although they classify correctly all the analysed modern mammalian communities among the major vegetational types. In fact, Reed (1998) did not test her discriminant functions with other modern communities not used in their adjustment, which constitutes a common procedure for assessing their robustness and predictive power (see detailed discussion in Mendoza et al., 2002).

These methodological problems could explain in part the contradictory results obtained by Reed (1998) in the paleosynecological reconstruction of the Makapansgat assemblages, and also her conclusions concerning the differences between the ecological structure of modern and fossil communities. In this paper, we will try to show that: (1) the trophic and size structure of mammalian communities constitutes an intrinsic property of the type of ecosystem, which is independent of its historical circumstances and taxonomic composition; and (2) discriminant analysis is a powerful tool for identifying those patterns. This

relates to the theoretical model proposed by Mendoza *et al.* (2004) for defining the underlying dynamics of communities as integrated dynamic systems, which makes it possible to explain the origin of common patterns in the structure of mammalian communities evolving in similar environmental conditions.

MATERIALS AND METHODS

The ecological structure of a large mammal community can be represented as a point in the theoretical ecospace defined by the number of species from each trophic category and body size group. If communities from the same ecosystem type tend to cluster in this ecospace, within a region clearly distinguishable from those of other mammalian communities assembled on different types of ecosystem, then it could be accepted that they share a common pattern in their trophic and body size structure. These patterns can be identified with the help of canonical discriminant analysis. Such an analysis provides discriminant functions that are linear combinations of the original variables (i.e. the number of species per trophic and size group), and which thereby maximize the separation between the multivariate means or group centroids of the community types compared in a multi-dimensional ecospace (Davis, 1986; Mendoza *et al.*, 2002). A mathematical representation of these patterns can be obtained if the corresponding function is set to define the location of each centroid. In this way, the discriminant functions can thus be considered as mathematical algorithms (i.e. detailed sequences of actions to perform to accomplish some task) that allow the inference of the ecological features of large mammal communities of the past.

Discriminant analysis is usually applied following the direct method, which incorporates all the variables considered in the study in the discriminant function. However, some of these variables can be irrelevant to the ecological patterns that characterize the groups compared or their information may be partially redundant. Thus, their inclusion in the discriminant function may obscure the interpretation of the patterns obtained (Mendoza *et al.*, 2002). Moreover, the inclusion of a high number of variables increases the probability of obtaining a discrimination based on the particular features of the samples compared (see above), instead of those general properties that really characterize the mammalian communities that inhabit each major vegetational type; this is especially true if the sample size is not large enough.

In contrast, the stepwise procedure for selection of variables to be incorporated to the discriminant function allows us to establish the level of contribution of the variables to the discrimination process. This may be controlled by adjusting the probability value (P) for the variables to be included in the discriminant function (P_{in}) and the corresponding one to be excluded (P_{out}). It is then expected that with low values for P_{in} and P_{out}, the number of variables selected for the discriminant function will be lower than with high values, although their level of statistical significance will be higher. In addition, in using this procedure the redundant information is eliminated and the complementary information of those variables that are poorly correlated by themselves with the type of ecosystem is maximized (see details in Mendoza *et al.*, 2002).

Moreover, when several analyses are performed, using different probability values (P_{in}/P_{out}) or starting from different sets of variables, this methodology offers an interesting possibility for selecting a set of discriminant functions that involve different combinations of variables. Each of these algorithms can be evaluated taking into account the following three basic criteria (Mendoza *et al.*, 2002): (1) the percentage of correct reclassifications obtained;

(2) the number of variables included in the discriminant functions and their statistical significance; and (3) their predictive power, which may be checked by applying them to new samples (i.e. to those not used for obtaining the algorithms) whose classification is previously known. However, given that these samples are useful for adjusting the algorithms, the logical procedure is to redefine the discriminant functions after this check, using all the samples belonging to known groups available. In any case, the predictive power of the algorithms can be also tested over samples that could not previously be classified with enough precision into one of the groups, given that the use of these samples in the adjustment of the discriminant functions is not recommended. The Statistical Package for the Social Sciences (SPSS) allows the leave-one-out cross-validation or U-method. Following this procedure, each sample is preliminarily reclassified with a discriminant function adjusted with all the remaining samples. The percentage of correct classifications obtained following this procedure may also be used as a fourth criterion for evaluating the fitness of the algorithms adjusted.

Taking into account all these considerations, a discriminant analysis is probably the best way for identifying the real patterns that underlie each group.

Variables

To obtain the trophic-size structure of each community, the large mammal species of each community were classified into one of 10 feeding categories, subdivided into different size classes. The size division values were determined from the distribution of gaps in a histogram distribution of body mass of all the species in the database (herbivore and carnivore examined independently), thus ensuring that species fell into discrete categories, and also avoiding classes lacking species or based only on one species. That subdivision led to 19 trophic-size groups being obtained, whose number of species was used as independent variables to perform the analyses. The resultant groups are as follows:

- *General grazers* (GG), feeding mainly on grasses. This category includes those ungulate species in which more than 75% grass is consumed throughout the year. This feeding group is further subdivided into two size classes: GGI (<300 kg) and GGII (>300 kg).
- *Fresh-grass grazers* (FG), feeding predominantly on fresh grass, which represents more than 75% of the diet. They were also subdivided into two size classes: FGI (<300 kg) and FGII (>300 kg).
- *Mixed feeders* (MF), which consume grass, leaves and shrubs; grass represents 25–75% of the diet. They were subdivided into four size classes: MFI (<65 kg), MFII (65–300 kg), MFIII (300–1000 kg) and MFIV (>1000 kg).
- *Browsers* (Br), feeding mainly on leaves and shrubs. These species consume <25% grass and <50% fruit, and were further subdivided into three size classes: BrI (<65 kg), BrII (65–300 kg) and BrIII (>300 kg).
- *Frugivores* (Fr), feeding mainly on fruits, flowers, mushrooms and other non-fibrous plant foods. This category includes those species in which grass represents <25% and fruit >50%; species of this trophic category were not further subdivided into size classes, as they mainly included small animals (<20 kg).
- *Omnivores* (Omn), feeding on non-fibrous vegetable matter, mushrooms and animal tissues. This feeding class was not further subdivided into size classes.

- *Hypercarnivores* (HC), which include predators consuming more than 70% of vertebrate flesh, with prey species of similar size or larger than themselves (Van Valkenburgh, 1988). They were subdivided into three body mass classes: HCI (<10 kg), HCII (10–20 kg) and HCIII (>20 kg).
- *Omnivores-carnivores* (OC), with a diet that includes <70% of vertebrate flesh (Van Valkenburgh, 1988), composed of small vertebrates, carrion, invertebrates, fruit and non-fibrous vegetable matter.
- *Bone crackers* (BC), either predatory or feeding on carrion. These species (hyenas) have the ability to access the bone marrow that is not available to other carnivores.
- *Primates* (Pr), the only group that does not correspond strictly to a feeding category. Although these species have folivorous, frugivorous or omnivorous diets, they were not further subdivided into such feeding classes because the information available did not specify their diet in the African communities with precision.

In the case of extinct herbivores, their feeding behaviour can be determined from their craniodental anatomy using the set of discriminant functions developed by Mendoza *et al.* (2002). Habitat preferences can be estimated using morphological variables of the postcranial skeleton (e.g. Kappelman *et al.*, 1997). Body masses can be estimated with regression equations adjusted for mass on morphological variables in modern ungulates (see chapters in Damuth and MacFadden, 1990). Moreover, the feeding habits, habitat preferences and body masses of extinct bovids can be estimated with more specific algorithms (M. Mendoza, C.M. Janis and P. Palmqvist, unpublished). In addition, stable isotopes and trace elements have been shown to be useful tools for paleodietary analysis (see review in Palmqvist *et al.*, 2003). The reconstruction of the predatory behaviour of extinct carnivores, and the estimation of their body masses, can also be addressed using combined biogeochemical and ecomorphological approaches (e.g. Van Valkenburgh, 1987; Anyonge, 1996; Biknevicius & Van Valkenburgh, 1996; Palmqvist *et al.*, 1999, 2002a).

Samples

In addition to the 86 large mammal communities from Africa, 24 communities from the Indo-Malaysian region in Asia were used. All these African and Asian communities are from protected areas (i.e. national parks, biosphere reserves, sanctuaries) or areas relatively undisturbed by man (e.g. some deserts or mountains) with relatively homogeneous environmental conditions (see Appendix). Most of their faunal lists were derived from internal, largely unpublished documents of the World Conservation Monitoring Centre (WCMC) in Cambridge, UK. Apart from these documents, maps of vegetational cover for Africa and the Indo-Malaysian realm were used for estimating the ecological features of each community. The maps were elaborated by the GIS Department of the WCMC, and include the limits of the protected areas considered in this study. These maps used information (available online at http://edcwww.cr.usgs.gov) from the Eros (Earth Resources Observation Systems) Data Centre, completed and checked with the IUCN Directories of Protected Areas for Tropical Africa and South Asia. All this information makes it possible to classify most of the African communities within one of the following ecological categories (see Appendix):

1. Treeless arid communities (TAC), including communities with low precipitation, sparse vegetation, without trees or with a few dispersed trees. This category does not include

those areas that have no trees due to edaphic reasons or causes other than aridity. Where possible, these communities were further subdivided into:

1.1. Semi-desert steppes and dry deserts (SD). These show very sparse or widely dispersed xerophytic vegetation, sometimes with shifting sand dunes that impede the growth of vegetation. Trees are completely absent.

1.2 Treeless arid or semi-arid communities (TAC) or bushlands. The vegetation is dominated by grasses and/or shrubs adapted to a long dry season, although a few dispersed, drought-adapted, deciduous tree species can grow, and tree patches can eventually emerge in the margins of the riparian habitats or surrounding water sources.

2. Woodlands (WS). There are wide ranges in precipitation and tree coverage in these areas. All of them share at least a yearly period of drought. According to their tree coverage, they were further subdivided into:

2.1. Open woodlands (OWS). These include those communities adapted to long periods of drought, with some trees showing adaptations for resistance to fire.

2.2. Closed woodlands (CWS). These sometimes include areas of deciduous forest and the most humid areas usually show characteristic intruding species from evergreen forests.

Note that while deciduous forests are present in Africa, they have been greatly depleted by human activities, and no community from a protected area could be classified as such in our database. For this reason, deciduous forests were not used as an independent ecological category.

3. Evergreen forests (EF). These are characterized by a continuous stand of evergreen or semi-evergreen trees at least 10 m tall. This category includes lowland, mountain and swamp forests, but not mangroves.

It is worth mentioning several potential sources of error and bias in this analysis. First, the lists of large mammal species that inhabit the national parks and other protected areas studied here are composite lists of every species that occurs in all the included habitat types. Although most parks are dominated by a specific habitat type, virtually none exclusively represents a single habitat, which implies that their faunal lists are inflated in variable proportions with species from other types of communities. To avoid the effects of mixing, the ecological features of the protected areas (i.e. plant cover, rainfall and temperature) and the species that inhabit them were carefully checked using reports, unpublished documents and books edited by the WCMC. This information allowed the exclusion of about 20% of the protected areas initially selected for analysis, as these areas showed a mixture of habitats whose relative extent was difficult to evaluate with precision on the maps of vegetation. As discussed in detail below, the discriminant functions project these 'mixed communities' (which were not used in the adjustment of the functions) in an intermediate region of the ecospace, between those communities dominated by the single habitats. This indicates that multi-habitat communities will represent a mixed trophic structure in the ecological patterns identified by the discriminant functions and in their representation in the multidimensional space. This mixed trophic structure is likely to be the case for most fossil assemblages, where there is almost always a variable degree of habitat averaging for taphonomic reasons (see reviews in Cutler *et al.*, 1999; Palmqvist *et al.*, 2002b).

Second, our classification of habitat types is less precise than other habitat classifications used specifically in Africa (e.g. Pratt *et al.*, 1966; Grunblatt *et al.*, 1989). The reason for this simplification is the need to compare the African large mammal communities analysed here with their equivalents in Asia. In addition, the ecological characterization of modern communities had to be precise enough to provide inferences for fossil assemblages that were also as precise as possible. Taking into account this compromise, only three general types of ecosystem were distinguished: evergreen forests, wooded savannas, and treeless arid communities with sparse vegetation. These types appear to correspond to the three main different types of ecological organization (Mendoza *et al.*, 2004). This reduction in possible ecosystems to three major habitat types allows the comparison of large mammal communities from different continents and time periods. In addition, the heterogeneity of the sources of information on the ecology of modern large mammal communities imposed clear limitations on this study. The information available from vegetation maps was also limited, and in most cases did not allow precise quantitative estimation of the relative surface of the parks covered by canopy trees or other types of vegetation.

Third, this study does not include the small mammal (<1 kg) species of the communities analysed, although their diversity seems to be better correlated with the extent of woody vegetation than is the diversity of large mammals (Andrews and O'Brien, 2000). One reason for excluding them relates to reference sources: the faunal lists of national parks and other protected areas generally do not include all the small mammal inhabitants. Another reason relates to the taphonomic biases: the bones of small mammals are more likely to be subjected to fragmentation by trampling, more rapid rates of weathering, and more complete destruction by carnivores than those of large mammals (Arribas and Palmqvist, 1998; Palmqvist *et al.*, 2002b). This preservational bias against small species is found when living communities are compared with Pleistocene or older assemblages (e.g. Wolff, 1975; Damuth, 1982), which precludes the use of small mammal assemblages for reconstructing past communities and vegetation. In any case, although the diversity of large mammal assemblages does not seem to correlate well with the extent of woody vegetation (Andrews and O'Brien, 2000), our analyses demonstrate that the three major types of vegetation are closely reflected in the distribution of large mammal species among size classes and feeding categories, which allows the inference of the synecological properties of extinct assemblages.

Following the considerations described above, only 68 of the 86 African communities were classified with enough precision into one of these three general ecological categories: these included 19 treeless arid communities with sparse vegetation, 27 wooded savannas and 22 humid evergreen forests. The remaining 18 communities either presented a mixture of types of vegetation from two of these categories or the information available on their ecology was not conclusive (see Appendix). Nineteen of the 24 Asian communities were classified into general ecological categories, but the reliability of these assignments is lower than for the African ones, and thus had to be complemented with information available from web-based sources (i.e. http://www.sanctuaryasia.com/projecttiger/bandipur.doc). Five of the Asian communities were classified as treeless arid communities, six as evergreen forests, and seven in a fourth ecological category that includes those communities in which the deciduous forest is the predominant habitat (DF; see Appendix). Note that the Asian communities are less suitable for these analyses than the African ones because their ecological homogeneity is often not guaranteed, and the information available about them and the species that inhabit them is more limited.

Statistical analysis

Different sets of statistical analyses were performed. A preliminary, descriptive factor analysis, using principal components as the method of extraction of eigenvectors, was applied to all African communities to determine whether their trophic-size structure was related to the type of ecosystem. This principal component analysis, which used the number of species of the 24 feeding-size groups as independent variables, allows the identification of the underlying factors that explain the configuration of the correlation matrix inside the group of variables (Davis, 1986; Norusis, 1988). This kind of analysis is very interesting because it does not use direct information about the identified factors, but uses only the information that is contained in the variables, in this case the number of species from each trophic-size group. However, discriminant analysis is most likely the best methodology for characterizing the ecological patterns in the trophic-size structure of the mammalian communities. Quadratic discriminant functions were used to identify the mammalian trophic-size patterns that characterize the three general types of ecosystems (i.e. treeless arid communities, wooded savannas and humid evergreen forests), using the 68 African communities that were previously classified into one of these categories (Table 1). The predictive power of the algorithms obtained was tested by the leave-one-out cross-validation method (see above) and also using the 18 non-classified African communities. These algorithms were then applied to the Asian communities to determine whether those belonging to a similar type of ecosystem share a common pattern in their trophic-size structure with the African communities, despite their differences in taxonomic composition.

Characteristic patterns from arid communities, wooded savannas and humid evergreen forests were also obtained with a joint discriminant analysis of African and Asian communities. Evergreen forests and arid communities from both continents were clustered into the same ecological category, respectively. However, the Asian deciduous communities were not used in the adjustment of the algorithms. One reason for this is because although some Asian communities have types of vegetation equivalent to those present in African wooded savannas, most of them include mainly deciduous forested areas that do not strictly correspond to any of the three general ecological categories established in our study. In addition, the low number of Asian deciduous forest communities, and the absence among them of communities with a single habitat type, did not allow the establishment of a new category of deciduous forest communities.

Two sets of discriminant analyses were also performed for a more precise characterization of both arid and wooded communities, respectively. Only those communities from Africa with more reliable ecological information were used in these analyses. The ecological categories used for characterizing their trophic-size structure are listed in Table 1, together with the discriminant functions that make their characterization possible.

Finally, the algorithms selected in all these analyses were applied to the paleosynecological reconstruction of the large mammal assemblage from Venta Micena (Palmqvist and Arribas, 2001). This locality is situated in the Guadix-Baza intra-montane basin (Granada, Southeast Spain), which was endorheoic (i.e. characterized by interior drainage) until late Pleistocene times, thus facilitating an exceptional record of Plio-Quaternary taphocoenoses of large mammals in swampy and lacustrine sediments. The sedimentary environment of Venta Micena is characterized by wide emerged areas and swampy marginal zones around the Pleistocene lake, with small shallow ponds. The bone assemblage lies on a caliche paleosol

Table 1. Quadratic discriminant functions among ecological categories

Groups compared	N	Alg	P_{in}	P_{out}	Discriminant function	Eigen-value	Wilks' λ	$R_A/R_B/R_C$
Treeless arid communities[A] vs. wooded savannas[B] vs. rainforest[C]	African communities	**1.1**	0.009	0.01	**Axis 1:** 3.728GG I $- 1.831$GG II $+ 0.125$Br I $- 0.303$Frg $- 1.515$Omn $+ 3.303$BC $- 0.403$GG I$^2 + 1.656$GG II$^2 + 0.356$MF II$^2 - 2.372$BC$^2 - 3.639$	20.521	0.006	1.277/4.343/−5.897
	$N_A = 19$ $N_B = 27$ $N_C = 24$				**Axis 2:** 0.826GG I $+ 3.725$GG II $- 0.449$Br I $+ 0.281$Frg $+ 1.095$Omn $+ 2.204$BC $- 0.049$GG I$^2 - 1.103$GG II$^2 - 0.232$MF II$^2 - 3.139$BC$^2 - 3.139$	6.847	0.127	−4.129/2.036/0.979
		1.2	0.009	0.01	**Axis 1:** 2.697GG I $+ 0.968$GG II $- 0.683$Frg $- 0.868$Omn $+ 4.472$BC $- 0.286$GG I$^2 + 0.045$Frg$^2 - 2.910$BC$^2 + 0.039$CO$^2 - 2.877$	15.006	0.010	0.331/4.485/−4.609
					Axis 2: 0.635GG I $+ 1.058$GG II I $+ 0.963$Frg $+ 1.571$Omn $+ 1.388$BC $- 0.042$GG I$^2 - 0.103$Frg$^2 - 1.378$BC$^2 - 0.089$CO$^2 - 2.827$	5.512	0.154	−3.480/1.680/1.363
	African and Asian	**2.1**	0.05	0.1	**Axis 1:** 2.599GG I $- 0.001$ MF IV $- 0.638$Frg $- 0.828$Omn $+ 4.255$BC $+ 0.125$CO $+ 0.201$FG $- 0.266$GG I$^2 + 0.678$GG II$^2 - 0.008$Br I$^2 + 0.044$Frg^2	16.132	0.007	0.061/4.781/−4.663
	$N_A = 24$ $N_B = 27$ $N_C = 28$				**Axis 2:** 0.566GG I $+ 1.072$ MF IV $+ 0.823$Frg $+ 1.704$Omn $+ 0.519$BC $- 0.507$CO $+ 0.241$FG $- 0.047$GG I$^2 + 0.272$GG II$^2 - 0.081$Br I$^2 - 0.090$Frg$^2 - 0.848$BC$^2 - 2.453$	6.874	0.127	−3.893/1.731/1.668
Dry deserts and semi-desert steppes[A] vs. treeless arid savannas[B] vs. arid savannas with some wooded areas[C]	$N_A = 7$ $N_B = 13$ $N_C = 7$	**3.1**	0.05	0.1	**Axis 1:** -7.157GG II $+ 2.431$MF II $+ 0.621$Br I $- 1.149$FG $+ 0.724$HC $- 1.962$	29.158	0.030	6.852/0.228/6.852
Arid savannas with some wooded areas[A] vs. open wooded savannas[B] vs. closed wooded savannas[C]	$N_A = 8$ $N_B = 24$ $N_C = 4$	**4.1**	0.05	0.1	**Axis 1:** 0.365Br I $- 1.117$Br III $+ 2.834$BC $+ 1.015$CO $- 0.267$Pr $- 3.487$	2.042	0.139	2.097/−0.236/−2.776
					Axis 2:: -0.777Br I $+ 0.543$Br III $+ 0.5374$BC $+ 0.623$CO $+ 0.592$Pr $- 2.071$	1.372	0.422	1.202/−0.769/2.209

Note: Alg., algorithm; P_{in}, P-value to be included; P_{out}, P-value to be excluded; test for Wilks' λ (all functions 0.00001); R, group centroids (R_A, R_B, R_C).

that surrounded the lake and is capped by 98–99% pure micritic limestone precipitated during a subsequent phase of water level rise (Arribas and Palmqvist, 1998).

Venta Micena is dated by biostratigraphy to the early Pleistocene, with an estimated age of 1.4 ± 0.1 Ma (Arribas and Palmqvist, 1999). The fossil assemblage is composed of a rich collection of approximately 6450 skeletal remains from 225 individuals belonging to 21 taxa of large (≥ 5 kg) mammals and about 10,000 unidentifiable bone shafts (Arribas and Palmqvist, 1998). Previous taphonomic research on the composition of this assemblage has shown that the skeletal remains were scavenged by the giant, short-faced hyena *Pachycrocuta brevirostris* from carcasses of ungulates preyed upon by flesh-eating carnivores (Palmqvist *et al.*, 1996). The selection by hypercarnivores of specific ungulates was basically a function of differences in the body masses of juvenile and adult prey individuals, as well as in the sex of prey. Major taphonomic biases in the preservation of the bone assemblage are related to the selective transport by hyenas of ungulate carcasses and body parts to their maternity dens, and with the preferential consumption of low-density, marrow-rich skeletal parts by adult and juvenile hyenas within the dens (Palmqvist and Arribas, 2001).

Autecological inferences on the feeding behaviour and habitat adaptations of these large mammals were derived from both ecomorphological and biogeochemical (trace elements abundance and stable isotope ratios) approaches. Size estimates were obtained by Palmqvist *et al.* (1996) using 'taxon-free' regression equations for body mass on craniodental and postcranial measurements in modern carnivore and ungulate species (see chapters in Damuth and MacFadden, 1990).

RESULTS AND DISCUSSION

Descriptive analysis

The first three factors of the principal component analysis (Fig. 2) clearly correspond to the three major ecological categories established here for African communities according to vegetational types. Together they account for 62% of the original variance, and show clearly that the structure of these mammalian communities, in terms of the distribution of species among feeding groups and size classes, is related to the general type of ecosystem.

Those communities showing a mixture of two vegetational categories usually have intermediate factor scores. For example, the mammalian communities that contain a mixture of treeless arid areas and wooded zones [i.e. those from Boule (BLE), Mago (MGO), Nechisar (NCH), Moremi (MRI), De Hoop (DHP) and the bushland and riverside forests of the Serengeti (SRB)], are all projected in intermediate positions between the samples of these two ecological categories on the scatter plots defined by the first three factors (Fig. 2). Buffalo (BFL), Okavango delta (OKV) and Gambella (GMB) are placed more closely to the wooded savannas, while Waza (WZA) is closer to the arid communities, but this is in accordance with those results obtained subsequently (see below). Similarly, the national parks of Comoe (CME), Outamba-Kilimi (OKL) and Marahoué (MRH), as well as the mountains of Loma (LMN) and Nimba (NMT), contain a mosaic of evergreen forests and closed humid savannas or Guinean savannas; all these communities are placed between evergreen forests and wooded savannas in the ecospace defined by the first three principal components (Fig. 2).
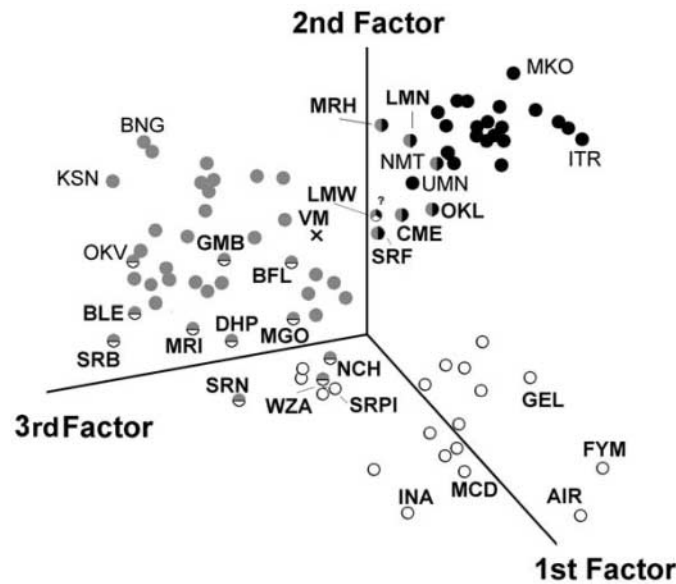
Fig. 2. Projection of African communities on the ecospace defined by the first three factors of the principal components analysis: solid circles, rainforests; grey circles, wooded savannas; open circles, arid communities without trees; cross, the early Pleistocene community from Venta Micena (VM, key for community abbreviations in Appendix).

Identification of ecological patterns

A first quadratic discriminant analysis was performed using only the African communities. The two algorithms with the greatest predictive power (1.1 and 1.2; Table 1) were selected. Both correctly reclassified all of the samples, even using the leave-one-out cross-validation method. These algorithms involve seven and six variables, respectively, which are all significant ($P < 0.01$ and, in most cases, $P < 0.001$). Thus, it appears that the discriminant functions obtained provide a good mathematical representation of the trophic-size pattern that characterizes the three general types of ecosystems in Africa.

Strong evidence of the predictive power of both algorithms is apparent in the fact that most of the ecologically mixed communities from Africa, which were not used in the algorithmic adjustment, are plotted in the appropriate position of the ecospace by these discriminant functions (Figs. 3, 4). This indicates, moreover, that the result of ecosystem mixing on the composition of the large mammal assemblage living in a given area reflects a similarly mixed trophic structure. In any case, the predictive power of algorithms obtained by the discriminant analyses was expected *a priori*, given the level of resolution obtained with factor analysis. However, what is really remarkable is the result obtained when these algorithms were applied to the Asian communities, whose species are completely different from those of Africa. Those Asian communities that share the same type of ecosystem with the African ones (e.g. evergreen forests and treeless arid communities) are situated close to their African equivalents. Asian deciduous communities (i.e. moist or dry monsoon deciduous forests, variably interspersed with grasslands), an ecosystem type with no clear
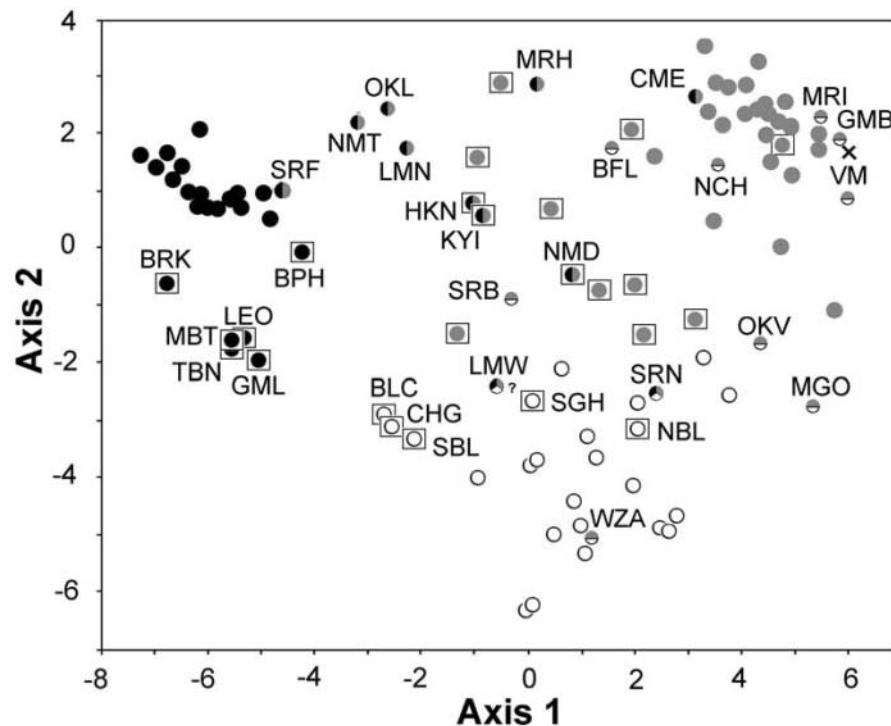
Fig. 3. Projection of African (circles) and Asian (boxed circles) communities on the ecospace defined by the two discriminant functions of algorithm 1.1, obtained using only African communities: solid circles, rainforests; grey circles, wooded savannas; open circles, treeless arid communities; cross, Venta Micena (VM, key for community abbreviations in Appendix).

African equivalent, are also appropriately placed around the African deciduous wooded savannas (see Figs. 3, 4), their ecosystem closest analogues.

These results show unequivocally a common pattern in the trophic-size structure among mammalian communities that inhabit the same ecosystem type, independent of their faunal composition. However, given that the algorithms obtained with the African communities do not classify the Asian ones with the same degree of accuracy, the pattern identified could in part be a consequence of the fact that those African communities of any particular ecosystem share many of their species because they are adapted to similar environmental conditions and they are not separated by important biogeographic barriers. In addition, it is also possible that the African and Asian ecosystems are not completely equivalent, because of continental-level climate differences (see Mendoza *et al.*, 2004). This led us to search more accurately for the patterns shared by both African and Asian communities, in spite of the fact that their species composition and historical circumstances are completely different. Thus, a new set of discriminant analyses among the three same general ecological categories was carried out, incorporating the Asian evergreen forests and arid communities with their African equivalents. Algorithm 2.1 (Table 1, Fig. 5) was selected among those obtained in these analyses, as it provides 100% correct reclassifications, even using the leave-one-out cross-validation method. The two quadratic discriminant functions of this algorithm involve 12 variables (Table 1).
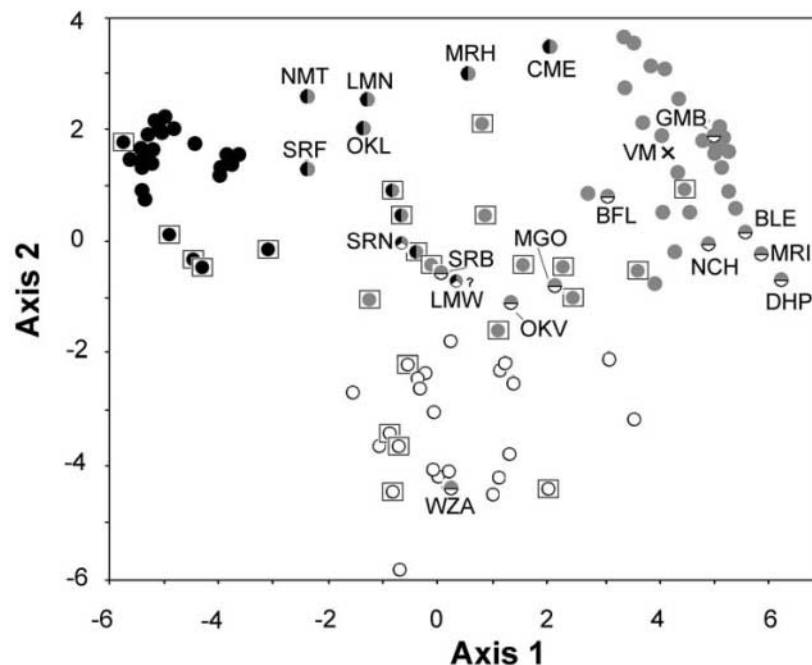
Fig. 4. Projection of African (circles) and Asian (boxed circles) communities on the ecospace defined by the two discriminant functions of algorithm 1.2, obtained using only African communities: solid circles, rainforests; grey circles, wooded savannas; open circles, treeless arid communities; cross, Venta Micena (VM, key for community abbreviations in Appendix).

A more detailed ecological characterization

The first sequence of non-quadratic discriminant analyses was carried out using all the African arid communities with sparse vegetation. These were subdivided into three ecological groups (see Appendix): (1) dry deserts (D) and semi-desert steppes (SD); (2) arid communities without tree coverage (TAC); and (3) arid communities that show some wooded areas (TAC/OWS). One algorithm was selected (3.1; Table 1) that involves six variables, all of them highly significant ($P < 0.01$), and correctly reclassifies 100% of the communities, even using the leave-one-out cross-validation method. Note that all of the discriminatory ability of this algorithm falls on the first discriminant axis, which explains more than 99% of the variance. This implies that the same variables differentiate the three ecological groups compared, and that the differences among these groups are only quantitative, probably because they share a similar type of organization (Mendoza *et al.*, 2004). This algorithm makes it possible to establish a gradient of aridity and plant coverage among the arid communities (Table 2). According to this gradient, the Aïr et du Ténéré National Park (AIR) would be the most arid community, with the least developed vegetational cover. This prediction seems to be correct, given that about 65% of the surface area of this park is covered by sand desert. The Waza National Park (WZA), which is apparently a mixed community with patches of treeless arid areas and open wooded areas, is classified by algorithm 3.1 as a completely arid community without tree coverage. Such a prediction fully agrees with the classification of this community by all previous algorithms.
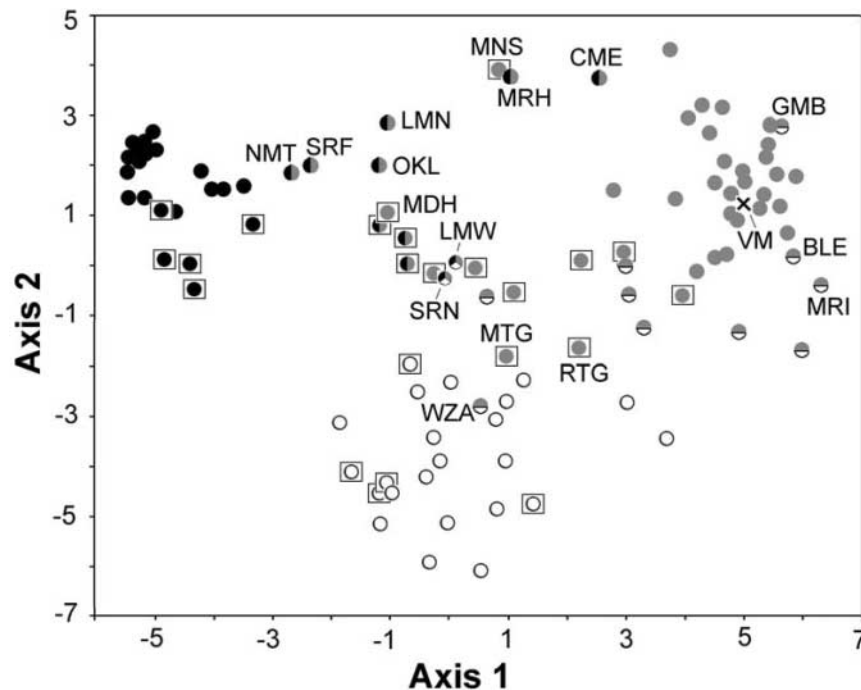
Fig. 5. Projection of African (circles) and Asian (boxed circles) communities on the ecospace defined by the two discriminant functions of algorithm 2.1, obtained in a joint analysis of African and Asian communities: solid circles, rainforests; grey circles, wooded savannas; open circles, treeless arid communities; cross, Venta Micena (VM, key for community abbreviations in Appendix).

Algorithm 3.1 was also applied to arid communities from Asia (Table 2). Unfortunately, the lack of precise knowledge of the vegetation of these communities makes it difficult to compare the results of this application with those of the African arid communities. In addition, almost none of these arid Asian communities correspond to undisturbed areas with natural boundaries and relatively homogeneous environmental conditions, because they usually correspond to territorial demarcations such as provinces (e.g. the Baluchistan province, BLC) or to specific areas within a given province (i.e. the North Baluchistan area, NBL, or the South Baluchistan area, SBL).

An additional sequence of non-quadratic discriminant analyses was performed using all of the deciduous wooded communities from Africa. The communities were clustered into the three following groups (see Appendix): (1) arid savannas that show some wooded areas (TAC/OWS); (2) open woodlands (OWS); and (3) closed woodlands (CWS). Again, only one algorithm was selected (4.1; Table 1), involving five variables, all of them significant ($P < 0.05$). In this algorithm, the discriminant ability of the first discriminant axis over the three groups is high (100% correct reclassifications, even using the leave-one-out cross-validation method), but the second one also plays an important role in the discrimination (Fig. 6). The first axis can be related to a gradient of tree coverage. According to this gradient, Bamingui Bangoran (BNG), a national park in the Central African Republic, would be the most densely wooded deciduous community, followed by the Gambella National Park (GMB). Gambella was previously classified as a mixed community with a

Table 2. Gradient of dryness and plant coverage among arid communities, established from the first discriminant axis of algorithm 3.1

Community	Ecosystem	Alg. 3.1	Community	Ecosystem	Alg. 3.1	Community	Ecosystem	Alg. 3.1
AIR	D/SD	9.67296	ASL	TAC	1.16007	WZA	TAC/OWS?	−0.44449
BLC	?	9.41341	YBL	TAC	1.12279	AWS	TAC	−0.77303
BEL	SD	7.5556	MKZ	TAC	0.99685	OMO	TAC	−0.77303
INA	SD	7.50118	CHG	?	0.93266	MRI	TAC/OWS	−6.31883
FYM	SD	6.77781	DJB	TAC	0.62499	BFL	TAC/OWS	−6.45244
NBL	?	6.51827	SWH	TAC	0.40524	SRB	TAC/OWS	−6.7835
MCD	SD	6.0536	YRS	TAC	0.27306	DHP	TAC/OWS	−7.38134
WCS	SD	5.32981	SRPI	TAC	0.20888	NCH	TAC/OWS	−7.50728
GEL	SD	5.07069	CHM	TAC	0.20888	BLE	TAC/OWS	−8.02595
SBL	?	4.08736	KMN	TAC	0.20012	MGO	TAC/OWS	−8.45705
SGH	?	1.19221	KRA	TAC	−0.24561			

Abbreviations: D, deserts; SD, semi-desert steppes; TAC, treeless arid communities; OWS, open wooded savannas (key for abbreviations in Appendix).
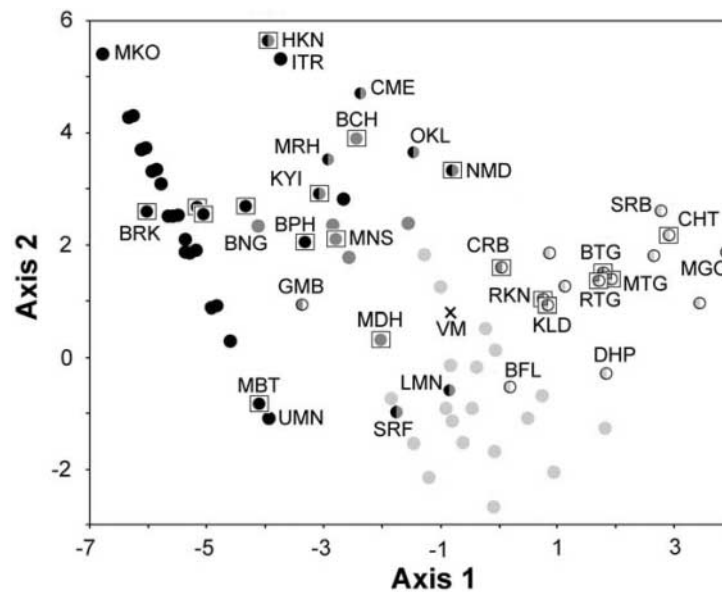
Fig. 6. Projection of African (circles) and Asian (boxed circles) communities on the ecospace defined by the two discriminant functions of algorithm 4.1: solid circles, rainforest; dark grey circles, moist, densely wooded deciduous communities; light grey circles, dry, open wooded communities; mixed grey and open circles, mixed communities with a mosaic of arid areas without trees and open wooded areas; cross, Venta Micena (VM, see key for abbreviations in Appendix).

mosaic of treeless arid areas and open wooded zones. However, its classification as a densely wooded community is in line with that made by all previous algorithms (Figs. 3–5) as well as with the position of this sample in the ecospace defined by the first three factors of the principal component analysis (Fig. 2). The reference in which its faunal list was obtained (Hillman, 1993) indicates that this park, situated in Ethiopia, contains xerophilous open savanna. In contrast, the IUCN Directory of Afrotropical Protected Areas describes it as combining open savanna grassland, woodland and even patches of deciduous forest. The second description seems to be the better one for this park according to the trophic-size structure of its mammalian community. Buffalo (BFL), which was classified as a typical wooded savanna by all algorithms and by its situation on the scatter diagram of the principal components analysis, is confirmed as an open wooded savanna by algorithm 4.1.

The predictive power of the first axis of algorithm 4.1 as a gradient of tree coverage is confirmed by the placement of the African and Asian rainforests. Although these forests are not deciduous, when they were tested with this algorithm they were all placed in the appropriate ecospace to the left of the most closed woodlands (Fig. 6).

Finally, algorithm 4.1 was applied to the deciduous communities from Asia. These communities are more appropriate than the arid ones for this comparative purpose, as most of them correspond to protected areas with natural boundaries and more homogeneous environmental conditions. According to the gradient of tree coverage that seems to represent the first discriminant axis, Chitwan (CHT) would be the community with the lowest degree of tree coverage. In fact, Chitwan National Park is a lush growth of short and long grass interspersed with patches of mixed forest. For a long time, the indigenous people that

inhabit the valley have been burning the grasslands during winter and early spring, in order to perpetuate them and discourage trees from moving in. Thus, fire and open grasslands appear to be inherently related to the ecology of Chitwan.

The three tiger reserves – Bandipur (BTG), Melghat (MTG) and Ranthambhore (RTG) – are also placed with the African open woodlands, followed by the Royal Karnali Reserve (RKN) and the Keoladeo National Park (KLD; Fig. 6). The three tiger reserves contain a tropical dry deciduous forest, whose coverage is fairly sparse and spread out, although some small humid areas are more densely covered by moist deciduous forest. The Royal Karnali Reserve (RKN) is bounded by numerous waterways of the Karnali River, which have created many large and small gravel islands. These islands are covered by a mosaic of grassland and riverine forest of acacia, sisam and the large buttressed silk cotton trees. The Keoladeo National Park (KLD) is a freshwater swamp, flooded in the monsoon season and surrounded by tropical dry deciduous forest, which is intermixed with dry grassland in those areas where the original forest has been degraded. Much of the area, however, is covered by medium-sized trees and shrubs (Navid, 1989).

The main vegetation of the Corbett National Park (CRB) is moist deciduous forest, intermixed with grasslands known locally as 'Chaurs'. Algorithm 4.1 places this park at the end of the range occupied by the mixed communities with patches of arid savannas and open woodlands, close to the moist open wooded savannas. Around 60% of the surface of the Madhupur National Park (MDH) is a closed, moist deciduous forest, and the remaining surface is an open deciduous forest. Algorithm 4.1 places it between the open and closed wooded savannas.

The two remaining Asian communities with deciduous forests, the Huai Kha Khaeng National Park (BCH) and the Manas Sanctuary (MNS), are placed among the moist, closed wooded savannas from Africa, which is appropriate given that these Asian communities contain moist deciduous forest. Namdapha (NMD) and Khao Yai (KYI), as well as the entire Huai Kha Khaeng (HKN), are mixed Asian communities with evergreen and moist deciduous forests. These parks, as well as those from Africa which also contain a similarly mixed vegetational type [i.e. Comoe (CME), Marahoué (MRH) and Outamba-Kilimi (OKL)], are projected by this algorithm at the same level as the closed woodlands, but in a somewhat higher position. However, the Loma Mountains (LMN) and the forests of the Serengeti (SRF), which also show a mosaic of vegetation, are situated among the open woodlands (Fig. 6).

Finally, the early Pleistocene large mammal assemblage from Venta Micena is unequivocally classified by principal components and algorithms based on discriminant functions as a typical deciduous woodland (Figs. 2–5). More specifically, algorithm 4.1 identifies this paleocommunity as an open woodland. These results agree well with those obtained recently in the paleoecological study of the large mammal assemblage preserved at this locality (Palmqvist *et al.*, 2003), using ecomorphological and biogeochemical approaches. Specifically, stable-isotope ratios (δ^{13}C, δ^{15}N, δ^{18}O) from bone collagen and trace-element abundance (Sr:Zn) in bone and tooth hydroxylapatite samples of these large mammals have made it possible to interpret their dietary niches and habitat preferences. These techniques reveal among ungulates the existence of: (1) grass-eating species in an open, savanna-like environment (e.g. horse *Equus altidens*, bison Bovini aff. *Leptobos*, and goat *Hemitragus albus*); (2) leaf-browsing ungulates in a closed, forested habitat (e.g. large megacerine deer *Eucladoceros giulii*, and rhino *Stephanorhinus etruscus*); and (3) mixed-feeding herbivores (e.g. ovibovine *Soergelia minor*, fallow deer *Dama* sp., and elephant *Mammuthus*

meridionalis) that probably dwelled in both plains and forests. Such paleoautecological inferences agree well with the mosaic of habitats (a relatively open, deciduous wooded community) inferred for this paleocommunity using the algorithms obtained with discriminant analysis for modern African communities.

CONCLUSIONS

The three major ecosystem types analysed here, which include rainforests, woodlands, and arid communities without tree coverage, show characteristic patterns in the trophic and size structure of the mammalian communities that inhabit them. These patterns are an intrinsic property of each type of ecosystem, independent of its specific historical circumstances and taxonomic composition. The clear definition of these different types of communities, which correspond with the first three vectors of the principal components analysis, demonstrates that these major ecosystem types correspond to three essential ways of organizing the land mammal-dominated ecosystems of Africa (see Mendoza *et al.*, 2004).

Within each major ecosystem type, each of which represents a basic organization of mammalian communities, the trophic and size structure of the mammalian communities is related to the degree of grass and shrub coverage among the arid communities, and to the extent of tree coverage among the deciduous wooded communities. The differences among the communities within each major ecosystem type affect the same faunal variables, in terms of body size and trophic structure, so it is possible to establish and characterize ecological gradients, which are also useful to obtain 'taxon-free' synecological inferences for extinct communities. However, the predictive power of the algorithms developed to identify these ecological gradients of vegetational coverage within each major ecosystem type is not as powerful as the ones that characterize the three major ecosystem types.

Finally, all the algorithms developed here unequivocally classify the large mammal assemblage from Venta Micena as being typical of an open woodland, which agrees well with the sedimentological, taphonomic and paleoecological information available on this early Pleistocene locality.

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APPENDIX

Large mammal communities analysed in this study

	Abbreviation	Ecosystem	Country
African communities			
Aïr et du Ténéré, Reserve	AIR	D, SD	Niger
kagera, National Park	AKG	OWS	Rwanda
Abijatta Shalla Lakes, National Park	ASL	TAC	Ethiopia
Awash, National Park	AWS	TAC	Ethiopia
Azagny, Reserve	AZG	EF	Ivory Coast
Babille Elephant, Sanctuary	BEL	TAC	Ethiopia
Buffalo, Reserve	BFL	TAC, OWS	Angola
Bwindi, National Park	BIM	EF	Uganda
Bikuar, National Park	BKR	OWS	Angola
Baoulé, Faunal Reserve	BLE	TAC, OWS	Mali
Benoué, National Park	BNE	CWS	Cameroon
Bamingui Bangoran, National Park	BNG	CWS	Cent. Afric. Rep.
Borgu, Game Reserve	BRG	OWS	Nigeria
Chimalavera, National Park	CHM	SD, TAC	Angola
Comoé, National Park	CME	CWS, EF	Ivory Coast
Conkouati, Reserve	CNK	EF	Congo
Diecke, Reserve forest	DCK	EF	Guinea
De Hoop, Reserve	DHP	(TAC, OWS)	South Africa
Djibouti (Country)	DJB	SD, TAC	Djibouti
Fayoum, Protected Area	FYM	SD	Egypt
Gebel Elba, protected Area	GEL	SD	Egypt
Gambella, National Park	GMB	OWS, TAC	Ethiopia
Iona, National Park	INA	SD	Angola
Ituri, National Park	ITR	EF	Zaire
Kafue, National Park	KFE	OWS	Zambia
Kameia, National Park	KMA	OWS	Angola
Kammanassie Mountains (Area)	KMN	TAC	South Africa
Kangandala, National Park	KNG	OWS	Angola
Kora National Reserve	KRA	TAC	Kenya
Korup, National Park	KRP	EF	Cameroon
Kisama, National Park	KSM	OWS	Angola
Kasungu, National Park	KSN	OWS	Malawi
Lame-Burra, Game Reserve	LBR	OWS	Nigeria
Lomami, National Park	LMI	EF	Zaire
Loma Mountains	LMN	EF, CWS	Sierra Leone
Lake Malawi, National Park	LMW	(F?, OWS, TAC)	Malawi
Luiana, Reserve	LNA	OWS	Angola
Luando, Reserve	LND	OWS	Angola
Lengwe, National Park	LNG	OWS	Malawi
Lopé, Reserve	LPE	EF	Gabon
Liwonde, National Park	LWN	OWS	Malawi
Mbini, Forest Reserve	MBN	EF	Equatorial Guinea
Mocamedes, Reserve	MCD	SD	Angola
Murchison Falls, National Park	MFL	CWS	Uganda
Mago, National Park	MGO	TAC, OWS	Ethiopia
Majete, Game Reserve	MJT	OWS	Malawi
Maiko, National Park	MKO	EF	Zaire
Mkomazi, Game Reserve	MKZ	TAC	Tanzania
Mupa, National Park	MPA	OWS	Angola

APPENDIX—*continued*

	Abbreviation	Ecosystem	Country
M′Passa-Makokou	MPK	EF	Gabon
Moremi Faunal Reserve, Forests	MRF	EF?	Botswana
Marahoué, National Park	MRH	CWS, EF	Ivory Coast
Moremi Faunal Reserve	MRI	TAC, OWS, F?	Botswana
Moremi Faunal Reserve, Savanna	MRS	OWS	Botswana
Mavinga, Reserve	MVN	OWS	Angola
Mwabvi, Game Reserve	MWB	OWS	Malawi
Nechisar, National Park	NCH	TAC, OWS	Ethiopia
Nkhotakota, Game Reserve	NKH	OWS	Malawi
Nimba Mount	NMT	EF, CWS	Guinea-Ivory C.
Nyika, National Park	NYK	OWS	Malawi
Oban, Forest	OBN	EF	?
Odzala, National Park	ODZ	EF	Congo
Outamba-Kilimi, National Park	OKL	CWS, EF	Sierra Leone
Okavango Delta	OKV	TAC, WS	Botswana
Omo, National Park	OMO	TAC	Ethiopia
Pendjari, National Park	PND	OWS	Benin
St. Floris, Reserve forest	SFL	CWS	Cent. Afric. Rep.
Salonga, National Park	SLN	EF	Zaire
Selous, Game Reserve	SLU	OWS	Tanzania
Serengeti Bushlands and Riverside Forests, NP	SRB	OWS, TAC	Tanzania
Serengeti Forests, National Park	SRF	EF, CWS?	Tanzania
Serengeti, National Park	SRN	EF, WS, TAC	Tanzania
Sarpo, National Park	SRP	EF	Liberia
Serengeti Plains, National Park	SRPl	TAC	Tanzania
Senkelle Swayne′s Hartebeest, Sanctuary	SWH	TAC	Ethiopia
Thai, National Park	TAI	EF	Ivory Coast
Mountains Usambar, Reserve forest	UMN	EF	Tanzania
Vwaza Marsh, Game Reserve	VMR	OWS	Malawi
Virunga Lowland Forests, National Park	VRF	EF	Zaire
Virunga Mountain forests, National Park	VRM	EF	Zaire
Virunga savannas, National Park	VRS	OWS	Zaire
West Coast, National Park	WCS	SD	South Africa
Waza, National Park	WZA	TAC, OWS,?	Cameroon
Yabello, Sanctuary	YBL	TAC	Ethiopia
Yangudi-Rassa, National Park	YRS	TAC	Ethiopia
Ziama, Reserve forest	ZMA	EF	Guinea
Asian communities			
Huai Kha Khaeng, Deciduous Forests	BCH	DF	Thailand
Baluchistan, Province	BLC	TAC	Pakistan
Huai Kha Khaeng, Rainforests	BPH	EF	Thailand
Berbak, Game Reserve	BRK	EF	Indonesia
Bandipur, Tiger Reserve	BTG	TAC, DF	India
Chagai desert, Area	CHG	TAC	Pakistan
Chitwan, National Park	CHT	OWS, DF	Nepal
Corbett, National Park	CRB	DF	India
Gunung Mulu, National Park	GML	EF	Malaysia
Huai Kha Khaeng	HKN	EF, DF, WS	Thailand
Keoladeo, National Park	KLD	DF	India
Khao Yai, National Park	KYI	DF, EF	Thailand
Lanjak-Entimau, Orang-utan Sanctuary	LEO	EF	Malaysia

APPENDIX—*continued*

	Abbreviation	Ecosystem	Country
Meru-Betiri, Reserve	MBT	EF	Indonesia
Madhupur, National Park	MDH	DF	Bangladesh
Manas, Sanctuary	MNS	(CWS, DF)?	India
Melghat, Tiger Reserve	MTG	DF	India
North Baluchistan, Area	NBL	TAC	Pakistan
Namdapha, National Park	NMD	EF, DF	India
Royal Karnali, Reserve	RKN	DF, ?	Nepal
Ranthambhore, Tiger Reserve	RTG	TAC	India
South Baluchistan, Area	SBL	TAC	Pakistan
Huai Kha Khaeng, Open Grasslands	SGH	TAC	Thailand
Tabin, Reserve	TBN	EF	Malaysia

Abbreviations: D, deserts; SD, semi-desert steppes; TAC, arid communities without trees; OWS, open wooded savannas; CWS, closed wooded savannas; EF, evergreen forests; DF, deciduous forests.