



Analytical framework for reconstructing heterogeneous environmental variables from mammal community structure



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ABSTRACT

We test the performance of two models that use mammalian communities to reconstruct multivariate palaeoenvironments. While both models exploit the correlation between mammal communities (defined in terms of functional groups) and arboreal heterogeneity, the first uses a multiple multivariate regression of community structure and arboreal heterogeneity, while the second uses a linear regression of the principal components of each ecospace. The success of these methods means the palaeoenvironment of a particular locality can be reconstructed in terms of the proportions of heavy, moderate, light, and absent tree canopy cover. The linear regression is less biased, and more precisely and accurately reconstructs heavy tree canopy cover than the multiple multivariate model. However, the multiple multivariate model performs better than the linear regression for all other canopy cover categories. Both models consistently perform better than randomly generated reconstructions. We apply both models to the palaeocommunity of the Upper Laetoli Beds, Tanzania. Our reconstructions indicate that there was very little heavy tree cover at this site (likely less than 10%), with the palaeo-landscape instead comprising a mixture of light and absent tree cover. These reconstructions help resolve the previous conflicting palaeoecological reconstructions made for this site.

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Introduction

The reconstruction of past environments is one of the key objectives of palaeoecology (Louys et al., 2012), with community-based (synecological) methods being a major contributor to this effort (Andrews et al., 1979; Nesbit-Evans et al., 1981; Andrews, 1989, 1996; Kay and Madden, 1997; Reed, 1997, 1998; Kovarovic et al., 2002; Mendoza et al., 2005; Reed and Russak, 2009; Louys et al., 2009; Muldoon, 2010; Louys and Meijaard, 2010; Meloro and Kovarovic, 2013). Synecological methods use the structure of animal communities defined either ecologically or taxonomically to determine the habitats occupied. Specifically, the ecological structure of any animal community can be expressed as an n -dimensional space, i.e., by n multiple discrete variables that describe how

the animals inhabit or utilise the environment or landscape in which they are found. The combination of these variables (= functional or taxonomic groups) describes the ecological space (ecospace) of the community.

The habitats that palaeoecologists seek to reconstruct are just as much multivariate ecospace as the animal communities that inhabit them. However, in palaeosynecological analyses, environments are usually not described or reconstructed in this way. Rather, in order to facilitate comparisons between modern and fossil communities, these habitats are discretely categorised. For example, habitats can be categorised as forests, woodlands, or grasslands, and this has largely been affected by the restrictions of the multivariate methods employed (e.g., principal components analysis, principal coordinates analysis, and discriminant function analysis). By using categorisations, palaeoecologists implicitly acknowledge that these are a means of partitioning a continuous multidimensional spectrum of environmental conditions into manageable units. However, the explicit reconstruction of the

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multidimensional nature of the palaeoenvironment on the basis of communities has so far remained elusive (although see [Cerling et al., \(2011\)](#) for a different approach to reconstructing multivariate environments using stable isotopes). We contend that this has been one contributor to the description of many palaeoenvironments as ‘mosaics’ or ‘mixed’ habitats.

Alternatively, habitats and environments can be described by any number of biotic and abiotic quantitative variables. This is the cornerstone of landscape and community ecology ([Jongman et al., 1995](#)). In a recent paper, we described the multivariate relationship that exists between arboreal heterogeneity and mammal community structure ([Louys et al., 2011](#)). We analysed two separate ecospace, mammal community and arboreal heterogeneity, both of which occupied the same geographical area. For a selection of sixty-three natural protected areas spread amongst the continents of Africa, Asia, and South and Central America, we determined the relative amounts of canopy cover of trees (arboreal heterogeneity) as well as the structure of the mammal community, in turn derived from species lists from those areas. The two separate ecospace—one vegetational and the other faunal—were compared both between and within continents, and the relationships between them explored. A linear and significant relationship between the ecological guild of small arboreal and semi-arboreal secondary consumers and the relative proportion of continuous canopy cover was found when all continents were considered together (the categories BAS and %Heavy, respectively, see [Table 1](#)). The amount of absent tree cover was also consistently correlated with mammal community structure, especially with relative percentage of large terrestrial primary consumers.

Here, we demonstrate how this relationship can be applied to the fossil record, exploring how mammal communities can be used to retrodict arboreal heterogeneity. Although in this paper we only retrodict arboreal heterogeneity as one multidimensional biotic variable, the methods we outline could easily be expanded to include other environmental biotic and abiotic variables. We provide an outline of the techniques that could be employed, as well as exploring the limitations of this new method.

Materials and methods

Abbreviations used in this study are listed in [Table 1](#). Ecospace were defined from information on sixty-three natural protected areas (NPAs) in Central and South America (hereafter ‘America,’ $n = 8$), Africa ($n = 23$), and Asia ($n = 32$). Mammalian species lists

Table 1
List of variables and their abbreviations used in this study.

Ecological guild/vegetation heterogeneity	
Small, arborophilic primary consumer	BAP
Small, arborophilic secondary consumer	BAS
Small, terrestrial primary consumer	BTP
Small, terrestrial secondary consumer	BTS
Medium arborophilic primary consumer	CAP
Medium, arborophilic secondary consumer	CAS
Medium, terrestrial primary consumer	CTP
Medium, terrestrial secondary consumer	CTS
Large, arborophilic primary consumer	DAP
Large, arborophilic secondary consumer	DAS
Large, terrestrial primary consumer	DTP
Large, terrestrial secondary consumer	DTS
Very large, arborophilic secondary consumer	EAS
Very large, terrestrial primary consumer	ETP
Very large, terrestrial secondary consumer	ETS
Relative proportion of heavy tree cover	%Heavy
Relative proportion of moderate tree cover	%Moderate
Relative proportion of light tree cover	%Light
Relative proportion of absent tree cover	%Absent

and geographical coordinates for NPAs were taken from the Man and the Biosphere Species Database (<http://ice.ucdavis.edu/mab>; see Supplementary Online Material [SOM]). The locations of these protected areas are shown in [Louys et al. \(2011: Fig. 1\)](#). Only species lists with more than 32 species were used; this number has been suggested as the likely minimum number necessary to confidently distinguish between three discrete and broadly defined habitat types across ecosystems (namely closed, mixed, and open; [Louys et al., 2009](#)). The palaeoecology of the Upper Laetolil Beds was examined on the basis of the new method described below. The faunal list for this site was obtained from published sources ([Harrison, 2011](#)).

Ecological categories and habitat classification

Following [Louys and Meijaard \(2010\)](#) and [Louys et al. \(2011\)](#), we restricted our faunal categorisation to three ecological categories: 1) body mass, divided into small (B; 1–10 kg), medium (C; 10–45 kg), large (D; 45–180 kg), and very large ($E > 180$ kg); 2) trophic level, primary (P) or secondary (S) consumer; 3) locomotion, either strictly terrestrial (T) or potential and strict arboreality (A; which we refer to hereafter as “arborophilic;” see below). Mammals with mean body mass less than 1 kg as well as all bats were removed, as these species sample and interact with the environment differently than larger arborophilic or terrestrial animals, and are less likely to be preserved in fossil assemblages alongside larger mammals ([Damuth, 1982](#)). Removing bats and tiny mammals follows the procedure set out in other synecological studies (e.g., [Andrews et al., 1979](#); [Kay and Madden, 1997](#); [Rodríguez, 2004](#); [Louys and Meijaard, 2010](#); [Louys et al., 2011](#)).

Our method uses a binary system when defining ecological guilds: a species either falls in one strictly defined category, or it does not. We use a very strict definition of terrestriality ([Louys et al., 2011](#)), such that animals with even implied arboreality are termed ‘arborophilic.’ For example, the porcupine (*Hystrix*) is not usually considered a tree dwelling species. However, [Nowak \(1999: 1647\)](#) states that the porcupine “does not usually climb trees,” implying that they can climb, and hence have arboreal capabilities. Therefore we would not classify this species as strictly terrestrial (T) in our analysis, but rather potentially arboreal, i.e., arborophilic (A). This definition encompasses not only mammals that are dependent on trees for survival but also those that may potentially use trees even sporadically, such as for predator avoidance or occasional food resources. We likewise use a very strict definition of primary consumer. Ecological data for modern species were taken from [Nowak \(1999\)](#). This reference is comprehensive and widely available, and using it as the source of information for all taxa helps to ensure consistency of classification. We provide a list of all modern species scored according to our scheme in the Supplementary Online Material ([Table 1 of SOM spreadsheet](#)).

The ecological categories described above were combined into fifteen discrete functional groups, and the relative proportion of each species in the community from each protected area was calculated. Our functional groups are less detailed than those used previously by other researchers (e.g., [Reed, 1997, 1998](#); [Kovarovic et al., 2002](#); [Mendoza et al., 2005](#); [Rodríguez et al., 2006](#); [Reed and Russak, 2009](#); [Moloro and Kovarovic, 2013](#)), however they still provide accurate retrodictions ([Louys and Meijaard, 2010](#)). Moreover, these functional groups are simple, binary (for trophic group and locomotion), and almost always unequivocal. As such, fossil taxa whose palaeobiologies are largely unknown and which share no modern analogues can be assigned to functional groups with a high degree of confidence.

Vegetation structure was classified following the method described by [Louys et al. \(2011\)](#). Using Google Earth we captured a

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