



# Diet and locomotion, but not body size, differentiate mammal communities in worldwide tropical ecosystems



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## ABSTRACT

**Aim:** To test whether tropical habitat groups across the world can be differentiated by using taxon-free mammalian community structures and to discuss the implications of this analysis for palaeoecological community studies.

**Materials and methods:** We used mammalian community data for 169 localities, which were assigned a priori to hierarchical Olson (1983) vegetation categories. Species over 500 g were classified into dietary, locomotion, and body mass groups and the resulting group structures were analysed using community structure analyses (NPMANOVA, CAP, SIMPER).

**Results:** The test results show that the mammalian community structures are significantly different between all of Olson's categories. These differences are highest at Olson's major and minor ecosystem levels, and require the least number of variable categories. At the vegetation level, the number of variable categories required to distinguish between them becomes higher. Of the dietary groups, the number of frugivore–granivores, frugivore–omnivores, grazers and mixed feeders contribute most to these differences, while the number of arboreal, arboreal–terrestrial and subterranean–terrestrial species are the key locomotor groups. Body mass was not a good discriminator.

**Main conclusions:** As general ecosystem categories are broken down into more precisely defined habitats, it requires more detailed knowledge of the species adaptations to distinguish between them. Many of Olson's vegetation groups represent a continuum of cover that are, at least at the worldwide comparison, too detailed to differentiate when broad generalities are sought. We suggest using three worldwide tropical major ecosystems in mammalian community structure analyses: "Humid, closed forests", "Seasonal or interrupted forests and grasslands", and "Seasonal, open drylands". Our results also demonstrate that community structures defined by both dietary and locomotor adaptations are powerful discriminators of tropical ecosystems and habitats across the continents we examined, but body mass should be interpreted with caution when the research question pertains to multiple continents.

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## 1. Introduction

The use of mammalian communities as proxies for past habitats and environmental conditions has a long established history (e.g. Andrews et al., 1979). Such synecological studies may employ a taxonomic approach in which communities with similar taxonomic compositions are considered to have inhabited analogous environments (Simpson, 1943; Fleming, 1973). However, a "taxon-free" approach is favoured by palaeoecologists concerned about the difficulties in identifying species in the fossil record and the assumption that fossil taxa behaved the same as their modern forms (Harrison, 1962; Andrews et al., 1979; Andrews and Hixson, 2014). Such studies focus on how the resident species exploit available spatial and trophic niches irrespective of taxonomic identity through an evaluation of each taxon's adaptations

to specific ecological variables, including dietary preferences and locomotor patterns.

Freed from the need to identify specific taxa, communities from different continents and time periods can be compared, giving us the tools to analyse past environmental changes, palaeoclimates and habitat distribution on a global scale. However, many mammalian community studies are restricted to a single geographical realm (e.g. Andrews et al., 1979; Reed, 1997, 1998; Mendoza et al., 2004), with few concentrating specifically on mammalian communities between continents (e.g. Kelt et al., 1996; Andrews and Humphrey, 1999; Rodríguez et al., 2006a). An implicit assumption in these studies is that mammalian communities from the same types of environment will have similar community structures between continents.

Comparisons of communities from different world regions can reveal global generalities, assuming that the relationship between size and abundance of species within specific geographical locations and habitats tells us something about the partitioning of resources in natural communities (Peters and Raelson, 1984; Fa and Purvis, 1997). For

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example, the distribution of species in various classes of body sizes, feeding adaptations, and food habits suggest that the structure of Old and New World tropical mammalian communities is very similar (Fleming, 1973). However, other research demonstrates that despite general resemblances communities from regions with similar climates can radically differ in certain features (Dubost, 1984; Fleagle and Reed, 1996; Fa and Purvis, 1997; Rodríguez et al., 2006a), possibly relating to historic effects. Ecosystems evolve over time (Olson, 1966; Andrews et al., 1979; Janis, 1993); tectonic, regional, historical and climatic processes may all play a role. Mountain uplift (e.g. the rainshadow cast by the uplift of the East African rift; blocking of the monsoonal winds to Central Asia by uplift of Himalayas), changes in oceanic circulation (opening of Drake's passage between Antarctica and Australia, resulting in a cold circumpolar current around Antarctica), closing of the Tethys sea in Late Miocene to form the Mediterranean, isolation (e.g. Australia with its unique fauna), interchange between continents (e.g. the Great American Interchange of the late Pliocene) and major ecosystem changes (e.g. the current arid configuration of Sahara at the end of the Holocene climatic optimum) each contribute to differences between regional species pools and vegetation (Janis, 1993; De Vivo and Carmignotto, 2004; Louys et al., 2011; Fortelius, 2013; Owen-Smith, 2013). This presents a challenge in distinguishing between historical and ecological factors in community structure (Endler, 1982) and likewise suggests that mammal community structures around the world will present some significant differences.

In light of this, we analyse modern mammalian community structures across the tropical belt of four continents: the Americas, Africa, Asia and Australia, which is frequently neglected. We address the following question: can tropical habitats across the world be differentiated on the basis of their mammalian community structures?

## 2. Methods

### 2.1. Localities

This study includes 169 extant tropical localities between 23° 30' N and 23° 30' S (Fig. 1, Appendix S1 in Supporting information) from previously published studies including Andrews et al. (1979) (n = 23), Andrews and Humphrey (1999) (n = 16), Reed (1997) (n = 18) and Reed (2008) (n = 8) and the database compiled by the National Center

for Ecological Analysis and Synthesis (NCEAS) Workshop on Mammalian Communities (see Badgley et al., 2001; van Dam et al., 2001; Damuth et al., 2002) (n = 100). This is supplemented by four unpublished localities from P. Andrews (n = 3) and K. Reed (n = 1). We endeavoured to use only communities comprised of more than 20 species to ensure completeness of the locality species lists, although in some cases (i.e. tundra and montaneous habitats) the number is naturally not likely to be this high (Appendix S1).

Coordinates for each locality were taken from Andrews et al. (1979), Andrews and Humphrey (1999), the NCEAS database and WDP, the World Database on Protected Areas (IUCN and UNEP, 2009). Site-specific references were also consulted (Appendix S1).

### 2.2. Vegetation categories

We used the vegetation classification system of the “Major World Ecosystem Complexes Ranked by Carbon in Live Vegetation” GIS dataset, which characterises the vegetative cover of the Earth's land surface in 0.5 by 0.5 degree grid cells (Olson et al., 1983, 1985). The classes can be applied across continents because the system explicitly uses natural vegetation categories without defaulting to generalised physiognomic categories or specific vegetation types (i.e. coconut groves) like those considered in other systems (White and UNESCO, 1983; Eiten, 1992; Lawesson, 1994).

Olson et al. (1983) organises vegetation categories into a hierarchical structure with six levels of increasing complexity. Our analyses are conducted at three different levels corresponding to Olson et al.'s (1983) third, fourth and sixth. Their third level, which describes the landscape, is a broad grouping which we call ‘major ecosystems’. The fourth we call ‘minor ecosystems’, which takes into account latitudinal and altitudinal effects. Their sixth level takes into account temperature, moisture and seasonality. For this we use the term ‘vegetation category’ (Table 1). We excluded seven categories associated with human impact and agriculture (Leemans et al., 1996) and 11 marginal categories that did not describe our localities. Detailed descriptions of selected categories are found in Olson et al. (1983).

Localities may cover tens or thousands of kilometres of space depending on whether they are national parks, small conservancies, etc. This is not unlike other community analyses (e.g. Reed, 1998; Mendoza et al., 2004). Although one can expect there to be some

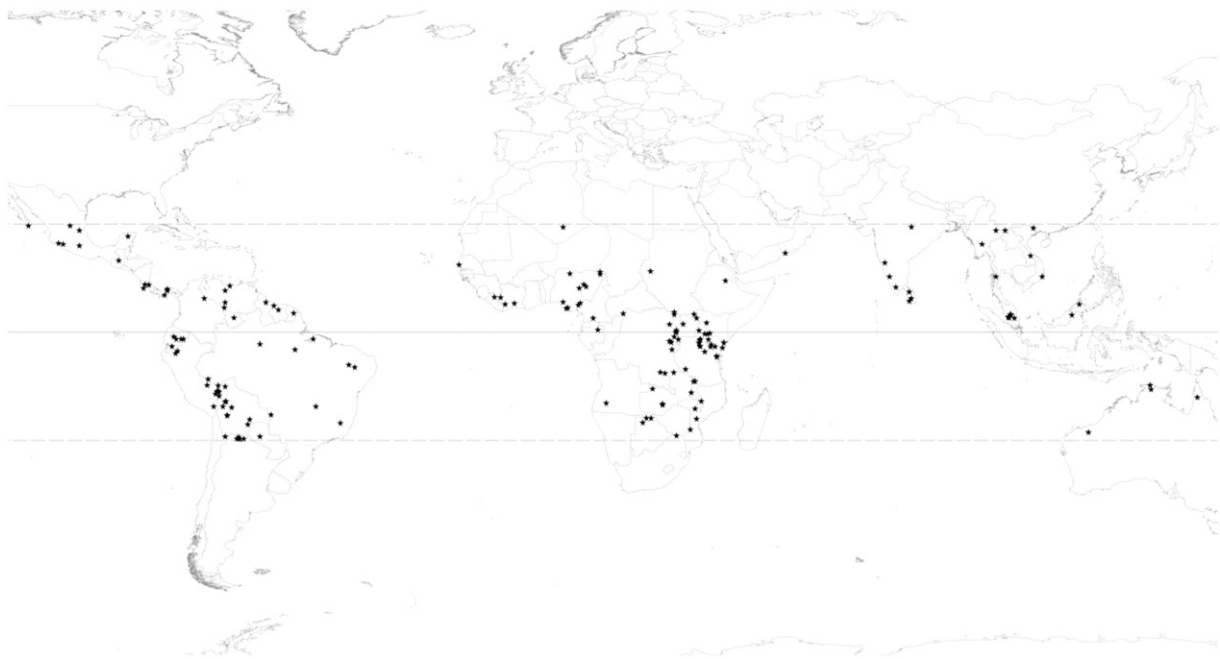


Fig. 1. 169 localities used in this study. For the list of names and coordinates see Appendix S1.

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