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.
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 & Humphrey, 1999; Rodríguez et al., 2006). 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 & Raelson, 1984; Fa and Purvis, 1997). For 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., 2006), 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 & 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 & Humphrey
(1999), the NCEAS database and WDPA, 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, 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 variation in topography and vegetation on the ground, especially where larger localities are concerned, our samples were selected for their relative homogeneity. Each locality was assigned to a vegetation category by comparing the detailed descriptions in our primary sources to those of Olson’s to further ensure that we were correct in our interpretation and that each of the localities did not include multiple broad vegetation complexes. The comparison was first made against the vegetation groups within the same grid cells where the localities are situated, then against the neighbouring ones, followed by those applicable to the tropical region of the locality’s country and finally for the whole country. The number of localities included in each vegetation category is summarised in Table 2.

2.3. **Locality species lists**

Species lists for each locality are derived from the published literature (Appendix S1; S2). We only consider species weighing more than 500g (n=607), as micromammals may be under-sampled in modern studies and are poorly represented in fossil sites. We restrict our analysis to non-volant mammals and exclude Chiroptera, Sirenia and Cetacea. This follows a well-established practice of excluding these groups in palaeoecommunity analyses due to the practical difficulties with including them as fossil species; they do not frequently fossilise or they are fossilised under very different taphonomic conditions compared to other, land-dwelling- or larger mammals. Given this, and their rarity in the fossil record, most workers thus exclude them (e.g. Andrews et al., 1979; Reed, 1998; Kovarovic et al., 2002; Mendoza et al., 2004; Louys et al., 2011). All of the species were matched against the taxonomy of Wilson and Reeder (2005).
2.4. Ecological variables

We assigned species to categories in four ecological variables: body mass, locomotor pattern, and two hierarchical dietary categories. These data are from NCEAS (Badgley et al., 2001; van Dam et al., 2001; Damuth et al., 2002), PanTHERIA (Jones et al. 2007) and MammalBase (Liow et al., 2008; Liow et al., 2009; Lintulaakso, 2013), a compilation of species attributes and diets based on hundreds of published sources.

2.4.1. Body mass

Taxa were assigned to a body mass category based on median body weights from several published sources (Appendix S2). Mass categories are modified from those in Andrews et al. (1979): 0.5-8 kg (A), 8-45 kg (B), 45-90 kg (C), 90-180 kg (D), 180-360 kg (E), and 360+ kg (F).

2.4.2. Locomotion

We divided the species into six locomotor groups which describe the substrate(s) in which the species moves (Reed, 1998; Miljutin, 2009): arboreal (A), arboreal-terrestrial (AT), subterranean (S), subterranean-terrestrial (ST), terrestrial (T) and terrestrial-aquatic (TA). If a species was found in several different references, the most common locomotion group among these was used (Appendix S2).
2.4.3. **Diet**

The dietary variable is divided into two levels of food resource preference (Table 3). Diet Level 1 represents the broadest categories of feeding strategy: animalivorous, frugivorous and herbivorous (Miljutin, 2009). Diet Level 2 follows that of Eisenberg (1981) with some modifications: mixed-feeders are added to the herbivore group, and aerial insectivores and foliage-gleaning insectivores are combined into one category: insectivores. As with locomotion, where a species was described in multiple references, the mostly frequently cited dietary preference was used (Appendix S2).

2.5. **Analysis**

Community structure data may be summarised in two ways: as raw counts of species in each category at each locality or converted to a percentage of the total number of species at each locality. Percentage data is common (Harrison, 1962; Fleming, 1973; Andrews et al., 1979; Reed 1997, 1998; Kovarovic et al., 2002; Louys, 2007; Louys et al., 2009; 2011), raw count data much less so (Mendoza et al., 2004, 2005; Rodríguez et al., 2006).

However, the use of percentages is potentially problematic because they generate a closed system (Aitchison 1986; Hernández & Vrba, 2006), giving rise to the so called ‘closure problem’ (Butler, 1981) in which the variables lack statistical independence (Jackson, 1997). It is most noticeable with few variables and decreases in magnitude as the number of variables is increased (Grayson, 1984; Jackson, 1997). As some of our analyses had only three groups, we use the number of species within each group transformed to \( \log_2(x) + 1 \) for \( x > 0 \), where \( x \) is the number of species (Anderson et al., 2006; decostand in R package vegan (Oksanen et al., 2007)). After transformation, a
Bray–Curtis distance matrix was calculated (Bray & Curtis, 1957; Legendre & Legendre, 1998). Analyses were conducted in R 3.0.0, using R-packages stats and vegan (Oksanen et al., 2007; R Development Core Team, 2005).

We tested spatial autocorrelation using the Mantel test (Mantel, 1967). Mantel r of association between Bray-Curtis dissimilarity and distance among sites ranged from a moderate of 0.43 (Mass) to a low of 0.16 (Locomotion) with randomization P-value of 0.001 (999 permutations, results not shown). Mantel correlograms showed that spatial correlation is highest in 414, 1243, 2072, and 2901 km class indices, i.e. localities which are closer together (within a continent) did tend to have more similar species composition. However, both CAP and NPMANOVA (see below) are non-parametric tests and, as such, are not affected by autocorrelation. If the observations are correlated with one another (e.g., temporally or spatially), then randomly shuffling them will eliminate this inherent structure, if it is present (Anderson, 2005). Therefore, a sensitivity analysis was performed using the original Bray-Curtis distance and the distance between NMDS space. The results were visualized with a Shepard plot (not shown here). For two axes (k=2), the resulting stress values were 0.09, 0.11, 0.12, and 0.15 for body mass, locomotion, diet level 1, and diet level 2 respectively. Values <0.1 correspond to a good ordination and values <0.2 still provide useful 2-dimensional ordination of the data (Clarke and Warwick, 2001).

We performed a constrained ordination (CAP, Canonical Analysis of Principal Coordinates; Anderson and Willis, 2003) to determine if there are differences among mammalian communities. CAP finds the canonical axis that best separates groups in multivariate space, and it also tests the hypothesis of no significant differences in multivariate location among groups. We plotted the product-moment correlation coefficient for each ecological
variable value with each of the canonical axes. High absolute correlation is interpreted as
an important factor for the nature of group differences (Anderson and Willis, 2003). A non-
parametric a priori test for differences among groups was also conducted using the
permutational multivariate analysis of variance (PERMANOVA or NPMANOVA; Anderson,
2001), followed by SIMPER (similarity percentage) which determines the relative
contribution of each ecological variable to the dissimilarity between groups (Clarke, 1993).
If a specific variable consistently contributes to both the within-group similarity and
between group dissimilarity, it is considered a good discriminator.

3. RESULTS

3.1. General analyses

Both the NPMANOVA and CAP test results show that the mammalian community
structures are significantly different between all categories (NPMANOVA, p<0.001, CAP,
P=0.005 Tables 4 & 5).

3.2. Ecological variable analyses

3.2.1. Diet

Most of the communities are significantly different between major ecosystems at both
dietary levels (NPMANOVA). In the CAP analysis, the number of frugivorous (mainly
frugivore-granivores and frugivore-omnivores) and herbivorous (grazer and mixed feeder)
species contribute most to the constrained ordination between major ecosystems (Fig. 2a).

SIMPER results indicate that the number of frugivorous species is important at Diet Level 1, and at Diet Level 2 frugivore-granivores contribute most to the dissimilarities between major ecosystem communities. As Olson's categories become more specific (i.e. major ecosystem to minor ecosystem to vegetation category), the number of dietary categories required to distinguish between them becomes higher (Table 6).

3.2.2. Locomotion

Between most of the category pairs, the mammalian community structures are significantly different (NPMANOVA). In the CAP analyses, the number of arboreal, arboreal-terrestrial and subterranean-terrestrial species contribute most to the differences (Fig. 2b). SIMPER results indicate that the number of arboreal or arboreal-terrestrial species is important for the dissimilarities between communities; the subterranean-terrestrial, terrestrial-aquatic, and terrestrial species contributed much less so (Table 7).

3.2.3. Mass categories

In NPMANOVA body mass categories were not as dissimilar between mammalian groups as the other variables. CAP shows that the number of small species contributes most to the group differences (Fig. 2c). In SIMPER, the number of large (360+ kg) and small (0.5-8 kg; 8-45 kg) species has the highest contribution to the dissimilarities between category pairs (Table 7).
3.3. Mammalian community structures in Olson’s categories

3.3.1. Major forest and woodland (FW) and sub-categories within it

FW differs from the other major ecosystems; the only exception is “major wetlands” (WL). It has the largest number of frugivorous and arboreal species compared with more open ecosystems “grass and shrub complexes” (GS) and “tundra and desert” (TD). SIMPER indicates that the lower number of herbivorous species in FW and the lower number of arboreal species in “interrupted woods” (IW) distinguish these two ecosystems.

At the minor ecosystem level, the “main tropical/subtropical forest” (TSF) had similar results as FW. The “mid-latitude broad-leaved and mixed forest” (MBF) differed from the IW ecosystems by having lower number of subterranean-terrestrial species. MBF had also fewer terrestrial species than “main grassland or shrubland” (MGS), and more arboreal-terrestrial species than “nonpolar desert or semidesert” (SDS).

At the vegetation level, TSF has three sub-groups. These groups are dissimilar between each other and most of the other vegetation groups. However, there were no significant differences between the “tropical dry forest and woodland” (RGD) vs. “tropical savanna and woodlands” (SGW) and “tropical/subtropical broad-leaved humid forest” (TBS) vs. “Tropical montane complexes” (TMC) pairs (Tables 6, 7).

3.3.2. Interrupted Woods (IW) and sub-categories within it
IW differed from the other major ecosystems, WL being the only exception. However, at
the minor ecosystem level, the “other dry woods mosaics” (DWM) could be differentiated
from the wetlands by having fewer arboreal species.

At the vegetation level, there were no significant differences between SGW and the “warm
or hot shrub and grassland” (MGS) nor between the SGW and RGD as mentioned earlier
(Tables 6, 7).

3.3.3. Grass and Shrub complexes (GS)

This major ecosystem had only one minor ecosystem and vegetation group, MGS. GS
differs from the other major ecosystems at some of the four community variables. At the
minor ecosystem level, MGS did not differ from “nonpolar desert or semidesert” (SDS)
and, at the vegetation level, MGS was not different from “tropical savanna and woodlands”
(SGW) or “desert and semidesert, (no winter snow)” (SDS) (Tables 6, 7).

3.3.4. Tundra and Desert (TD) and sub-categories within it

TD differs from the other major ecosystems. It had the least number of species in all of the
community variables. TD is divided into two minor ecosystems, SDS and “tundra, arctic
desert and ice” (TUN¹), but they do not differ. As mentioned above, MGS and SDS were
similar with each other, but MGS and TUN were not (Tables 6, 7).

3.3.5. Major Wetlands (WL)

¹The only localities from TUN were high Alpine tundra localities from South America.
This major ecosystem had only one vegetation category, “warm or hot wetlands, swamp/marsh” (SWP). WL is the only major ecosystem that does not differ from FW and IW. At the vegetation level, it can only be differentiated from forested (TBS, TRF) or open habitats (SDS, TUN) (Tables 6, 7).

4. DISCUSSION

We tested whether tropical habitats across the world can be differentiated on the basis of their mammalian community structures. Generally, our results show that the diet and locomotion categories differentiate the communities best, while body mass performed poorly. As Olson’s categories become more tightly defined, the number of ecological variable groups required for differentiation becomes higher. Differences between treeless categories, such as desert and grasslands, are not significant.

4.1. Ecological variables

Differences noted between dietary categories are largely accounted for by the number of frugivores. At Diet Level 2, this signal comes from frugivore-granivores (FG) and frugivore-herbivores (FH) (but see ordination in CAP where frugivore-omnivores are also important, Fig. 2a). Many of these species are primates but there are other frugivorous groups, such as ungulates, also present in high numbers in tropical forests which are under-represented in open habitats such as savannas and grasslands (Bodmer, 1990).

Others have found that the separation of vegetation groups relates more to the
grazer/browser continuum, rather than the abundance of frugivores (Sponheimer et al., 1999; Janis et al., 2000). In our study, the number of herbivores (mainly grazers and browsers in SIMPER, grazers and mixed-feeders in the CAP ordination) is important only at the minor ecosystem and vegetation level where “interrupted woods” (IW) and treeless areas like grasslands and tundra, are differentiated from each other. Animalivorous groups do not impact on the differences between major or minor ecosystems but, at the vegetation level, the low number of carnivorous species in MGS distinguishes this habitat from RGD. Similar results were obtained by Reed (1997, 1998) where frugivores, fruit/insect eaters and grazers discriminated between habitats with no clear contribution from animalivorous taxa. Herbivores and frugivores are mainly primary or secondary consumers while animalivores are higher in the trophic hierarchy. This may be the reason why habitats are reflected more by their primary and secondary consumers and the ‘signal’ from the primary production weakens towards the top of the trophic hierarchy.

When we compare results between Diet Level 1 and 2, the differentiation of the major and minor ecosystems and the vegetation categories is based on similar variables which relate to the abundance of frugivores and herbivores. The differences are more nuanced when we consider Diet Level 2, with between one and six variables required to distinguish between various habitat pairs. The broader classification (i.e. Diet Level 1), requiring a consideration of only frugivory and herbivory, may make it a more robust approach for worldwide ecosystem and vegetation comparisons, although clearly less detail is captured.

In terms of the locomotion groups, the number of arboreally adapted species differentiates closed (FW, IW) from open habitats (GS, TD). This is a conclusion borne out by many others (Reed 1997; Louys et al., 2011) who also demonstrate that an abundance of
arboreal species indicates the presence of well-developed tree cover. Primates and tree-
dwelling rodents comprise the majority of these taxa. The higher number of terrestrial-
aquatic species in wetlands (WL) only separated it from TD; otherwise WL did not
differentiate from FW and IW. We conjecture that the species lists from wetlands include
taxa from nearby areas that periodically visit for drinking and maybe counted as
inhabitants of both areas because they are observed in each. Interestingly, the number of
terrestrial species contributed very little to the differences between community structures in
SIMPER. Terrestriality may be too general of a category for describing species that move
about on the land surface. By adding more detailed locomotor classes (i.e. cursorial), the
separation between open and closed habitats could be clearer. In the CAP analysis, the
number of subterranean-terrestrial and terrestrial species did distinguish between humid
and forested localities (TBS, TRF) and seasonal or less forested areas (RGD, STW, SGW,
MGS). Seasonality and the inconsistent availability of food throughout the year can be
dealt with in two ways: migration, which requires terrestrial movement, or by caching food
resources, which subterranean-terrestrial species generally do.

Body mass categories did not clearly differentiate community structures, particularly in
vegetation categories. This may be a consequence of the scale of the investigation. Work
by Brown and Maurer (1989) has shown that the frequency distribution of body sizes
appears to be general; it is modal and skewed towards smaller species when large areas
(i.e. continents or biomes) are sampled, whereas there are approximately equal numbers
of species in each size category in smaller, local areas. They suggest that a strong
negative interaction prevents local coexistence of similar-sized species, so one would
therefore not expect that community structures could be distinguished at this scale.
However, further analysis of the data showed that the size ranges of mammals differed on
each continent. Africa has a higher proportion of larger mammals, whilst America and Australia have smaller species with Asia somewhere in between (Fig. 2d). This pattern is also observable in the palaeontological record of the Pleistocene and is likely to have roots deep in time (Janis 1993; De Vivo and Carmignotto 2004; Louys et al., 2011; Fortelius 2013; Owen-Smith 2013).

We found that only the number of small (0.5-8 kg, 8-45 kg) and large (360+ kg) species has the highest contribution (SIMPER) for some of the community pairs. The importance of small species is likely that, as a group, there is more variety in both dietary preferences and locomotion. Large species are almost always terrestrial herbivores, separating grasslands and savannas from forests, whereas small species can be arboreal, terrestrial, subterranean, as well as insectivores, frugivores, and herbivores. Although a recent study (M. Rodríguez et al., 2006) has shown that body size can be useful, this is only clear at higher latitudes suggesting that the warmer the annual temperature, the less likely body size is helpful in distinguishing habitats.

4.2. Distinguishing Olson’s categories

Generally, major ecosystems can be differentiated by the dietary and locomotor adaptations of their constituent species, but body mass is not a robust discriminator. For example, mass does not differentiate the FW-IW-GS continuum. This is likely to relate to historical differences between the continents that have resulted in unique body size ranges that are not correlated with habitat (Louys et al., 2011).
Minor ecosystems, particularly forested areas, are the easiest to distinguish from other categories. However, some pairs share similar mammalian community structures. These include MGS-SDS and SDS-TUN. Most of these are open environments that gradually transform into each other across the landscape and are likely to share species that are comfortably adapted to ecotones and a wider array of ecological conditions.

At the detailed level of vegetation category, the general pattern of differences between forested and open areas are still noticeable: the number of frugivorous and arboreal species account for most of the differences. However, the same types of pairs that did not differentiate at the minor ecosystem level can now be distinguished. These include SGW-RGD; SGW-MGS; TMC-TBS; MGS-SDS and SDS-TUN. The division of the minor ecosystem TSM into SGW and TMC reveals the true nature of this group: SGW represents more open and seasonal areas and TMC is more forested. This may be the reason why SGW does not clearly differ from RGD and MGS. Both SGW and RGD have some number of dry months during the year, are widespread and often mixed vegetation complexes (Olson et al., 1983). SGW is a mosaic that contains dry, grassy areas as well as places that are similar to tropical seasonal forests. On the other hand, RGD may also alternate with grassy savannas, so that points of separation become arbitrary (Olson et al., 1983). In the constrained ordination (CAP), RGD plotted near or within the SGW, STW, and MGS, which indicates that seasonality plays a major role for the mammalian composition of this vegetation group. TMC consists of rainy forests that may be locally denser than nearby lowlands and are more similar to woodlands, such as RGD (Olson et al., 1983). Other studies have subsumed montane forests into a general forest category (e.g. Reed, 1998). Although Olson classifies TMC as a part of interrupted woods (due to lower mean carbon density), our results also suggest that the community structure of TMC is similar to forest
complexes and that it is not appropriate to consider this habitat a part of IW.

4.3. Palaeoecological implications

Our study confirms that palaeoecological reconstructions of tropical fossil localities based on dietary and locomotor variables can be obtained. Questions raised regarding the appropriateness of modern comparative datasets derived from localities across multiple continents are possibly unwarranted, unless body size has been given significant consideration. This is not to say that ecological differences between the continents do not exist in the structure of communities. We showed some body mass differences with results similar to others (e.g. Smith et al., 2004; Louys et al., 2011), particularly in demonstrating that Africa has a higher number of large-bodied taxa; our tentative suggestion is that the differences are perhaps more meaningful than other workers who emphasise that body size distributions across continents are not significant (e.g. Smith et al., 2004). For example, during the drier late Pleistocene last glacial maximum, the body mass groups of mammalian faunas in South America and Africa were quite similar. However, during the wetter Holocene climatic optimum there was a decrease in open vegetation areas that lead to the loss of larger-sized mammal lineages in South America, whilst they survived in Africa. As a result, today Africa is richer in the number of species above 5 kg (De Vivo and Carmignotto 2004). In addition, Louys et al., (2011) hypothesise that faunal exchange over the past several million years between Africa and Asia contributes to community convergence, whereas the much longer separation of the New World from the Old World relates to differences between their communities. Furthermore, they posit that historical factors function on a much longer temporal scale in shaping community structure, which
suggests that some caution is warranted in selecting comparative communities from across the world for palaeoecological reconstructions of sites located on a continent that has been long separated from the others, or for analyses involving deep time. This can be interpreted from our results, too. Although we did not analyse continental differences in the other ecovariables, our results show only relatively small numbers of similar mammalian community structures within worldwide tropical vegetation classes. This indicates that historical and ecological factors are shaping mammalian community structure slightly differently in relatively similar primary production environments. (Endler 1982).

In addition to caveats regarding the usefulness of body mass as a habitat discriminator, our results provide an additional principal observation for palaeoecological community studies. Some vegetation groups represent a continuum of cover (TMC-TBS-TRF, RGD-SGW-MGS-SDS) that are, at least at the worldwide comparison, too detailed to differentiate when broad generalities are sought. This may be related to the methodology, in which habitats on this continuum are forced into discrete categories for the sake of analysis. The ecological reality is that differences between these groups are probably much more subtle than these discrete categories can be analysed using our ordination-based approaches and other common tests. One way around this problem may be to focus on reconstructing not habitat categories specifically, but the variable amount of canopy cover available in them, as Louys, et al., 2015 have done. However, one may seek more ecological detail than this, whereby the use of well-defined habitat categories is both convenient and analytically manageable. Where this option is pursued, we suggest using three worldwide tropical major ecosystems: “Humid, closed forests” that contains TMC, TBS, and TRF; “Seasonal or interrupted forests and grasslands” that contains RGD, SGW, and STW; and “Seasonal, open drylands” that contains MGS, SDS, and TUN (TBC and SWP were difficult to differentiate from the other groups so they are excluded from our
three groups; the former exists mostly in mid-latitudes and is a marginal habitat in the Tropics, whilst the latter is a generalised category that can be found naturally within many other habitats). These broad groups are similar in structure to those described by Mendoza et al. (2004): “evergreen forests”, “wooded savannahs that share grass and browse” and “arid communities with sparse plant cover”. They identified these in strictly African communities, but they appear to hold at the global level, as well, further highlighting their utility in ecological reconstructions. Interestingly, these authors do not consider locomotion in their study, but assign each large mammal taxon to a group which combines feeding strategy and body size.

The data as we have analysed them herein demonstrate their wide applicability in distinguishing between modern habitats and, by extension, fossil localities where relatively complete species lists can be obtained. We appreciate that defining palaeospecies is not a straightforward task, but since we find that more precise habitat reconstructions are every bit as possible as broad ecosystem discrimination where increasingly detailed species information is analysed, palaeontological research should continue to approach questions of individual species adaptive complexes, as well as palaeocommunity structures and habitat affiliations.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1**: 169 localities from within the tropical belt

**Appendix S2**: Locality species and ecological variable assignments