1 **RESEARCH PAPER**

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3 Diet and locomotion, but not body size, differentiate mammal communities in worldwide

4 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

47   requires more detailed knowledge of the species adaptations to distinguish between them.

48   Many of Olson's vegetation groups represent a continuum of cover that are, at least at the

49   worldwide comparison, too detailed to differentiate when broad generalities are sought. We

50   suggest using three worldwide tropical major ecosystems in mammalian community

51   structure analyses: "Humid, closed forests", "Seasonal or interrupted forests and

52   grasslands", and "Seasonal, open drylands". Our results also demonstrate that community

53   structures defined by both dietary and locomotor adaptations are powerful discriminators

54   of tropical ecosystems and habitats across the continents we examined, but body mass

55   should be interpreted with caution when the research question pertains to multiple

56   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 & 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.

98   Comparisons of communities from different world regions can reveal global generalities,

99   assuming that the relationship between size and abundance of species within specific

100   geographical locations and habitats tells us something about the partitioning of resources

101   in natural communities (Peters & Raelson, 1984; Fa and Purvis, 1997). For example, the

102   distribution of species in various classes of body sizes, feeding adaptations, and food

103   habits suggest that the structure of Old and New World tropical mammalian communities is

104   very similar (Fleming, 1973). However, other research demonstrates that despite general

105   resemblances communities from regions with similar climates can radically differ in certain

106   features (Dubost, 1984; Fleagle and Reed, 1996; Fa and Purvis 1997; Rodríguez *et al*.,

107   2006), possibly relating to historic effects. Ecosystems evolve over time (Olson, 1966;

108   Andrews *et al*., 1979; Janis 1993); tectonic, regional, historical and climatic processes may

109   all play a role. Mountain uplift (e.g. the rainshadow cast by the uplift of the East African rift;

110   blocking of the monsoonal winds to Central Asia by uplift of Himalayas), changes in

111   oceanic circulation (opening of Drake's passage between Antarctica and Australia,

112   resulting in a cold circumpolar current around Antarctica), closing of the Tethys sea in Late

113   Miocene to form the Mediterranean, isolation (e.g. Australia with its unique fauna),

114   interchange between continents (e.g. the Great American Interchange of the late Pliocene)

115   and major ecosystem changes (e.g. the current arid configuration of Sahara at the end of

116   the Holocene climatic optimum) each contribute to differences between regional species

117   pools and vegetation (Janis 1993; De Vivo and Carmignotto 2004; Louys et al., 2011;

118   Fortelius 2013; Owen-Smith 2013). This presents a challenge in distinguishing between

119   historical and ecological factors in community structure (Endler 1982) and likewise

120   suggests that mammal community structures around the world will present some

121   significant differences.

122

123   In light of this, we analyse modern mammalian community structures across the tropical

124   belt of four continents: the Americas, Africa, Asia and Australia, which is frequently

125   neglected. We address the following question: can tropical habitats across the world be

126   differentiated on the basis of their mammalian community structures?

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132   **2. METHODS**

133   **2.1. Localities**

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135   This study includes 169 extant tropical localities between 23° 30 N and 23° 30 S (Fig. 1,

136   Appendix S1 in Supporting Information) from previously published studies including

137   Andrews, *et al* (1979) (n= 23), Andrews & Humphrey (1999) (n=16), Reed (1997) (n=18)

138   and Reed (2008) (n=8) and the database compiled by the National Center for Ecological

139   Analysis and Synthesis (NCEAS) workshop on Mammalian Communities (see Badgley *et*

140   *al*. 2001; van Dam *et al*. 2001; Damuth *et al*. 2002) (n=100). This is supplemented by four

141   unpublished localities from P. Andrews (n=3) and K. Reed (n=1). We endeavoured to use

142   only communities comprised of more than 20 species to ensure completeness of the

143   locality species lists, although in some cases (i.e. tundra and montaneous habitats) the

144   number is naturally not likely to be this high (Appendix S1).

145

146   Coordinates for each locality were taken from Andrews *et al*. (1979), Andrews & Humphrey

147 (1999), the NCEAS database and WDPA, the World Database on Protected Areas (IUCN

148 and UNEP 2009). Site-specific references were also consulted (Appendix S1).

149

150   2.2.   **Vegetation categories**

151

152 We used the vegetation classification system of the "Major World Ecosystem Complexes

153 Ranked by Carbon in Live Vegetation" GIS dataset, which characterises the vegetative

154 cover of the Earth's land surface in 0.5 by 0.5 degree grid cells (Olson *et al.*, 1983, 1985).

155 The classes can be applied across continents because the system explicitly uses natural

156 vegetation categories without defaulting to generalised physiognomic categories or

157 specific vegetation types (i.e. coconut groves) like those considered in other systems

158 (White, 1983; Eiten, 1992; Lawesson, 1994).

159

160 Olson *et al.* (1983) organises vegetation categories into a hierarchical structure with six

161 levels of increasing complexity. Our analyses are conducted at three different levels

162 corresponding to Olson *et al.*'s (1983) third, fourth and sixth. Their third level, which

163 describes the landscape, is a broad grouping which we call '*major ecosystems*'. The fourth

164 we call '*minor ecosystems*', which takes into account latitudinal and altitudinal effects.

165 Their sixth level takes into account temperature, moisture and seasonality. For this we use

166 the term '*vegetation category*' (Table 1). We excluded seven categories associated with

167 human impact and agriculture (Leemans *et al*, 1996) and 11 marginal categories that did

168 not describe our localities. Detailed descriptions of selected categories are found in Olson

169 *et al.* (1983).

170

171 Localities may cover tens or thousands of kilometres of space depending on whether they

172 are national parks, small conservancies, etc. This is not unlike other community analyses

173 (e.g. Reed, 1998; Mendoza *et al.,* 2004). Although one can expect there to be some

174 variation in topography and vegetation on the ground, especially where larger localities are

175 concerned, our samples were selected for their relative homogeneity. Each locality was

176 assigned to a vegetation category by comparing the detailed descriptions in our primary

177 sources to those of Olson's to further ensure that we were correct in our interpretation and

178 that each of the localities did not include multiple broad vegetation complexes. The

179 comparison was first made against the vegetation groups within the same grid cells where

180 the localities are situated, then against the neighbouring ones, followed by those

181 applicable to the tropical region of the locality's country and finally for the whole country.

182 The number of localities included in each vegetation category is summarised in Table 2.

183

184   2.3.   **Locality species lists**

185

186 Species lists for each locality are derived from the published literature (Appendix S1; S2).

187 We only consider species weighing more than 500g (n=607), as micromammals may be

188 under-sampled in modern studies and are poorly represented in fossil sites. We restrict our

189 analysis to non-volant mammals and exclude Chiroptera, Sirenia and Cetacea. This

190 follows a well-established practice of excluding these groups in palaeoecommunity

191 analyses due to the practical difficulties with including them as fossil species; they do not

192 frequently fossilise or they are fossilised under very different taphonomic conditions

193 compared to other, land-dwelling- or larger mammals. Given this, and their rarity in the

194 fossil record, most workers thus exclude them (e.g. Andrews *et al*., 1979; Reed, 1998;

195 Kovarovic *et al*., 2002; Mendoza *et al.,* 2004; Louys *et al.,* 2011). All of the species were

196 matched against the taxonomy of Wilson and Reeder (2005).

197

2.4.   **Ecological variables**

199

200 We assigned species to categories in four ecological variables: body mass, locomotor

201 pattern, and two hierarchical dietary categories. These data are from NCEAS (Badgley *et*

202 *al.,* 2001; van Dam *et al.,* 2001; Damuth *et al.,* 2002), PanTHERIA (Jones *et al.* 2007) and

203 MammalBase (Liow *et al.,* 2008; Liow et al., *2009;* Lintulaakso, 2013), a compilation of

204 species attributes and diets based on hundreds of published sources.

205

206

2.4.1. *Body mass*

208

209 Taxa were assigned to a body mass category based on median body weights from several

210 published sources (Appendix S2). Mass categories are modified from those in Andrews *et*

211 *al.* (1979): 0.5-8 kg (A), 8-45 kg (B), 45-90 kg (C), 90-180 kg (D), 180-360 kg (E), and

212 360+ kg (F).

213

2.4.2. *Locomotion*

215

216 We divided the species into six locomotor groups which describe the substrate(s) in which

217 the species moves (Reed, 1998; Miljutin, 2009): arboreal (A), arboreal-terrestrial (AT),

218 subterranean (S), subterranean-terrestrial (ST), terrestrial (T) and terrestrial-aquatic (TA). If

219 a species was found in several different references, the most common locomotion group

220 among these was used (Appendix S2).

221

222   2.4.3. *Diet*

223

224   The dietary variable is divided into two levels of food resource preference (Table 3). Diet

225   Level 1 represents the broadest categories of feeding strategy: animalivorous, frugivorous

226   and herbivorous (Miljutin, 2009). Diet Level 2 follows that of Eisenberg (1981) with some

227   modifications: mixed-feeders are added to the herbivore group, and aerial insectivores and

228   foliage-gleaning insectivores are combined into one category: insectivores. As with

229   locomotion, where a species was described in multiple references, the mostly frequently

230   cited dietary preference was used (Appendix S2).

231

232   2.5.   **Analysis**

233

234   Community structure data may be summarised in two ways: as raw counts of species in

235   each category at each locality or converted to a percentage of the total number of species

236   at each locality. Percentage data is common (Harrison, 1962; Fleming, 1973; Andrews *et*

237   *al.*, 1979; Reed 1997, 1998; Kovarovic *et al.*, 2002; Louys, 2007; Louys *et al.*, 2009; 2011),

238   raw count data much less so (Mendoza *et al.*, 2004, 2005; Rodríguez *et al.*, 2006).

239   However, the use of percentages is potentially problematic because they generate a

240   closed system (Aitchison 1986; Hernández & Vrba, 2006), giving rise to the so called

241   'closure problem' (Butler, 1981) in which the variables lack statistical independence

242   (Jackson, 1997). It is most noticeable with few variables and decreases in magnitude as

243   the number of variables is increased (Grayson, 1984; Jackson, 1997). As some of our

244   analyses had only three groups, we use the number of species within each group

245   transformed to $\log_2(x) + 1$ for $x > 0$, where x is the number of species (Anderson *et al.*,

246   2006; decostand in R package vegan (Oksanen *et al.*, 2007)). After transformation, a

247 Bray–Curtis distance matrix was calculated (Bray & Curtis, 1957; Legendre & Legendre,

248 1998). Analyses were conducted in R 3.0.0, using R-packages *stats* and *vegan* (Oksanen

249 *et al.*, 2007; R Development Core Team, 2005).

250

251 We tested spatial autocorrelation using the Mantel test (Mantel, 1967). Mantel r of

252 association between Bray-Curtis dissimilarity and distance among sites ranged from a

253 moderate of 0.43 (Mass) to a low of 0.16 (Locomotion) with randomization P-value of

254 0.001 (999 permutations, results not shown). Mantel correlograms showed that spatial

255 correlation is highest in 414, 1243, 2072, and 2901 km class indices, i.e. localities which

256 are closer together (within a continent) did tend to have more similar species composition.

257 However, both CAP and NPMANOVA (see below) are non-parametric tests and, as such,

258 are not affected by autocorrelation. If the observations are correlated with one another

259 (e.g., temporally or spatially), then randomly shuffling them will eliminate this inherent

260 structure, if it is present (Anderson, 2005). Therefore, a sensitivity analysis was performed

261 using the original Bray-Curtis distance and the distance between NMDS space. The results

262 were visualized with a Shepard plot (not shown here). For two axes (k=2), the resulting

263 stress values were 0.09, 0.11, 0.12, and 0.15 for body mass, locomotion, diet level 1, and

264 diet level 2 respectively. Values <0.1 correspond to a good ordination and values <0.2 still

265 provide useful 2-dimensional ordination of the data (Clarke and Warwick, 2001).

266

267 We performed a constrained ordination (CAP, Canonical Analysis of Principal Coordinates;

268 Anderson and Willis, 2003) to determine if there are differences among mammalian

269 communities. CAP finds the canonical axis that best separates groups in multivariate

270 space, and it also tests the hypothesis of no significant differences in multivariate location

271 among groups. We plotted the product-moment correlation coefficient for each ecological

272   variable value with each of the canonical axes. High absolute correlation is interpreted as

273   an important factor for the nature of group differences (Anderson and Willis, 2003). A non-

274   parametric *a priori* test for differences among groups was also conducted using the

275   permutational multivariate analysis of variance (PERMANOVA or NPMANOVA; Anderson,

276   2001), followed by SIMPER (similarity percentage) which determines the relative

277   contribution of each ecological variable to the dissimilarity between groups (Clarke, 1993).

278   If a specific variable consistently contributes to both the within-group similarity and

279   between group dissimilarity, it is considered a good discriminator.

280

281

282   ## 3. RESULTS

283

284   ### 3.1. General analyses

285

286   Both the NPMANOVA and CAP test results show that the mammalian community

287   structures are significantly different between all categories (NPMANOVA , $p<0.001$, CAP,

288   P=0.005 Tables 4 & 5).

289

290   ### 3.2. Ecological variable analyses

291

292   #### 3.2.1. *Diet*

293

294   Most of the communities are significantly different between major ecosystems at both

295   dietary levels (NPMANOVA). In the CAP analysis, the number of frugivorous (mainly

296   frugivore-granivores and frugivore-omnivores) and herbivorous (grazer and mixed feeder)

297 species contribute most to the constrained ordination between major ecosystems (Fig. 2a).

298 SIMPER results indicate that the number of frugivorous species is important at Diet Level

299 1, and at Diet Level 2 frugivore-granivores contribute most to the dissimilarities between

300 major ecosystem communities. As Olson's categories become more specific (i.e. major

301 ecosystem to minor ecosystem to vegetation category), the number of dietary categories

302 required to distinguish between them becomes higher (Table 6).

303

304   3.2.2. *Locomotion*

305

306 Between most of the category pairs, the mammalian community structures are significantly

307 different (NPMANOVA). In the CAP analyses, the number of arboreal, arboreal-terrestrial

308 and subterranean-terrestrial species contribute most to the differences (Fig. 2b). SIMPER

309 results indicate that the number of arboreal or arboreal-terrestrial species is important for

310 the dissimilarities between communities; the subterranean-terrestrial, terrestrial-aquatic,

311 and terrestrial species contributed much less so (Table 7)

312

313

314   3.2.3. *Mass categories*

315

316 In NPMANOVA body mass categories were not as dissimilar between mammalian groups

317 as the other variables. CAP shows that the number of small species contributes most to

318 the group differences (Fig. 2c). In SIMPER, the number of large (360+ kg) and small (0.5-8

319 kg; 8-45 kg) species has the highest contribution to the dissimilarities between category

320 pairs (Table 7).

321

322

3.3. **Mammalian community structures in Olson's categories**

324

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

326

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.

332

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).

338

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).

344

3.3.2. *Interrupted Woods (IW) and sub-categories within it*

346

347 IW differed from the other major ecosystems, WL being the only exception. However, at

348 the minor ecosystem level, the "other dry woods mosaics" (DWM) could be differentiated

349 from the wetlands by having fewer arboreal species.

350

351 At the vegetation level, there were no significant differences between SGW and the "warm

352 or hot shrub and grassland" (MGS) nor between the SGW and RGD as mentioned earlier

353 (Tables 6, 7).

354

355   3.3.3. *Grass and Shrub complexes (GS)*

356

357 This major ecosystem had only one minor ecosystem and vegetation group, MGS. GS

358 differs from the other major ecosystems at some of the four community variables. At the

359 minor ecosystem level, MGS did not differ from "nonpolar desert or semidesert" (SDS)

360 and, at the vegetation level, MGS was not different from "tropical savanna and woodlands"

361 (SGW) or "desert and semidesert, (no winter snow)" (SDS) (Tables 6, 7).

362

363   3.3.4. *Tundra and Desert (TD) and sub-categories within it*

364

365 TD differs from the other major ecosystems. It had the least number of species in all of the

366 community variables. TD is divided into two minor ecosystems, SDS and "tundra, arctic

367 desert and ice" (TUN[1]), but they do not differ. As mentioned above, MGS and SDS were

368 similar with each other, but MGS and TUN were not (Tables 6, 7).

369

370   3.3.5. *Major Wetlands (WL)*

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[1] The only localities from TUN were high Alpine tundra localities from South America.

371

372 This major ecosystem had only one vegetation category, "warm or hot wetlands,

373 swamp/marsh" (SWP). WL is the only major ecosystem that does not differ from FW and

374 IW. At the vegetation level, it can only be differentiated from forested (TBS, TRF) or open

375 habitats (SDS, TUN) (Tables 6, 7).

376

377   4. **DISCUSSION**

378

379 We tested whether tropical habitats across the world can be differentiated on the basis of

380 their mammalian community structures. Generally, our results show that the diet and

381 locomotion categories differentiate the communities best, while body mass performed

382 poorly. As Olson's categories become more tightly defined, the number of ecological

383 variable groups required for differentiation becomes higher. Differences between treeless

384 categories, such as desert and grasslands, are not significant.

385

386   4.1.   **Ecological variables**

387

388 Differences noted between dietary categories are largely accounted for by the number of

389 frugivores. At Diet Level 2, this signal comes from frugivore-granivores (FG) and frugivore-

390 herbivores (FH) (but see ordination in CAP where frugivore-omnivores are also important,

391 Fig. 2a). Many of these species are primates but there are other frugivorous groups, such

392 as ungulates, also present in high numbers in tropical forests which are under-represented

393 in open habitats such as savannas and grasslands (Bodmer, 1990).

394

395 Others have found that the separation of vegetation groups relates more to the

396 grazer/browser continuum, rather than the abundance of frugivores (Sponheimer *et al.*,

397 1999; Janis *et al.*, 2000). In our study, the number of herbivores (mainly grazers and

398 browsers in SIMPER, grazers and mixed-feeders in the CAP ordination) is important only

399 at the minor ecosystem and vegetation level where "interrupted woods" (IW) and treeless

400 areas like grasslands and tundra, are differentiated from each other. Animalivorous groups

401 do not impact on the differences between major or minor ecosystems but, at the vegetation

402 level, the low number of carnivorous species in MGS distinguishes this habitat from RGD.

403 Similar results were obtained by Reed (1997, 1998) where frugivores, fruit/insect eaters

404 and grazers discriminated between habitats with no clear contribution from animalivorous

405 taxa. Herbivores and frugivores are mainly primary or secondary consumers while

406 animalivores are higher in the trophic hierarchy. This may be the reason why habitats are

407 reflected more by their primary and secondary consumers and the 'signal' from the primary

408 production weakens towards the top of the trophic hierarchy.

409

410 When we compare results between Diet Level 1 and 2, the differentiation of the major and

411 minor ecosystems and the vegetation categories is based on similar variables which relate

412 to the abundance of frugivores and herbivores. The differences are more nuanced when

413 we consider Diet Level 2, with between one and six variables required to distinguish

414 between various habitat pairs. The broader classification (i.e. Diet Level 1), requiring a

415 consideration of only frugivory and herbivory, may make it a more robust approach for

416 worldwide ecosystem and vegetation comparisons, although clearly less detail is captured.

417

418 In terms of the locomotion groups, the number of arboreally adapted species differentiates

419 closed (FW, IW) from open habitats (GS, TD). This is a conclusion borne out by many

420 others (Reed 1997; Louys *et al.*, 2011) who also demonstrate that an abundance of

421 arboreal species indicates the presence of well-developed tree cover. Primates and tree-

422 dwelling rodents comprise the majority of these taxa. The higher number of terrestrial-

423 aquatic species in wetlands (WL) only separated it from TD; otherwise WL did not

424 differentiate from FW and IW. We conjecture that the species lists from wetlands include

425 taxa from nearby areas that periodically visit for drinking and maybe counted as

426 inhabitants of both areas because they are observed in each. Interestingly, the number of

427 terrestrial species contributed very little to the differences between community structures in

428 SIMPER. Terrestriality may be too general of a category for describing species that move

429 about on the land surface. By adding more detailed locomotor classes (i.e. cursorial), the

430 separation between open and closed habitats could be clearer. In the CAP analysis, the

431 number of subterranean-terrestrial and terrestrial species did distinguish between humid

432 and forested localities (TBS, TRF) and seasonal or less forested areas (RGD, STW, SGW,

433 MGS). Seasonality and the inconsistent availability of food throughout the year can be

434 dealt with in two ways: migration, which requires terrestrial movement, or by caching food

435 resources, which subterranean-terrestrial species generally do.

436

437 Body mass categories did not clearly differentiate community structures, particularly in

438 vegetation categories. This may be a consequence of the scale of the investigation. Work

439 by Brown and Maurer (1989) has shown that the frequency distribution of body sizes

440 appears to be general; it is modal and skewed towards smaller species when large areas

441 (i.e. continents or biomes) are sampled, whereas there are approximately equal numbers

442 of species in each size category in smaller, local areas. They suggest that a strong

443 negative interaction prevents local coexistence of similar-sized species, so one would

444 therefore not expect that community structures could be distinguished at this scale.

445 However, further analysis of the data showed that the size ranges of mammals differed on

446   each continent. Africa has a higher proportion of larger mammals, whilst America and

447   Australia have smaller species with Asia somewhere in between (Fig. 2d). This pattern is

448   also observable in the palaeontological record of the Pleistocene and is likely to have roots

449   deep in time (Janis 1993; De Vivo and Carmignotto 2004; Louys *et al.,* 2011; Fortelius

450   2013; Owen-Smith 2013).

451

452   We found that only the number of small (0.5-8 kg, 8-45 kg) and large (360+ kg) species

453   has the highest contribution (SIMPER) for some of the community pairs. The importance of

454   small species is likely that, as a group, there is more variety in both dietary preferences

455   and locomotion. Large species are almost always terrestrial herbivores, separating

456   grasslands and savannas from forests, whereas small species can be arboreal, terrestrial,

457   subterranean, as well as insectivores, frugivores, and herbivores. Although a recent study

458   (M. Rodríguez *et al.*, 2006) has shown that body size can be useful, this is only clear at

459   higher latitudes suggesting that the warmer the annual temperature, the less likely body

460   size is helpful in distinguishing habitats.

461

462   4.2.   **Distinguishing Olson's categories**

463

464   Generally, major ecosystems can be differentiated by the dietary and locomotor

465   adaptations of their constituent species, but body mass is not a robust discriminator. For

466   example, mass does not differentiate the FW-IW-GS continuum. This is likely to relate to

467   historical differences between the continents that have resulted in unique body size ranges

468   that are not correlated with habitat (Louys *et al.*, 2011).

469

470   Minor ecosystems, particularly forested areas, are the easiest to distinguish from other

471   categories. However, some pairs share similar mammalian community structures. These

472   include MGS-SDS and SDS-TUN. Most of these are open environments that gradually

473   transform into each other across the landscape and are likely to share species that are

474   comfortably adapted to ecotones and a wider array of ecological conditions.

475

476   At the detailed level of vegetation category, the general pattern of differences between

477   forested and open areas are still noticeable: the number of frugivorous and arboreal

478   species account for most of the differences. However, the same types of pairs that did not

479   differentiate at the minor ecosystem level can now be distinguished. These include SGW-

480   RGD; SGW-MGS; TMC-TBS; MGS-SDS and SDS-TUN. The division of the minor

481   ecosystem TSM into SGW and TMC reveals the true nature of this group: SGW represents

482   more open and seasonal areas and TMC is more forested. This may be the reason why

483   SGW does not clearly differ from RGD and MGS. Both SGW and RGD have some number

484   of dry months during the year, are widespread and often mixed vegetation complexes

485   (Olson *et al.,* 1983). SGW is a mosaic that contains dry, grassy areas as well as places

486   that are similar to tropical seasonal forests. On the other hand, RGD may also alternate

487   with grassy savannas, so that points of separation become arbitrary (Olson *et al.,* 1983). In

488   the constrained ordination (CAP), RGD plotted near or within the SGW, STW, and MGS,

489   which indicates that seasonality plays a major role for the mammalian composition of this

490   vegetation group. TMC consists of rainy forests that may be locally denser than nearby

491   lowlands and are more similar to woodlands, such as RGD (Olson *et al.,* 1983). Other

492   studies have subsumed montane forests into a general forest category (e.g. Reed, 1998).

493   Although Olson classifies TMC as a part of interrupted woods (due to lower mean carbon

494   density), our results also suggest that the community structure of TMC is similar to forest

495   complexes and that it is not appropriate to consider this habitat a part of IW.

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497   **4.3.   Palaeoecological implications**

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499   Our study confirms that palaeoecological reconstructions of tropical fossil localities based

500   on dietary and locomotor variables can be obtained. Questions raised regarding the

501   appropriateness of modern comparative datasets derived from localities across multiple

502   continents are possibly unwarranted, unless body size has been given significant

503   consideration. This is not to say that ecological differences between the continents do not

504   exist in the structure of communities. We showed some body mass differences with results

505   similar to others (e.g. Smith *et al.,* 2004; Louys *et al.,* 2011), particularly in demonstrating

506   that Africa has a higher number of large-bodied taxa; our tentative suggestion is that the

507   differences are perhaps more meaningful than other workers who emphasise that body

508   size distributions across continents are not significant (e.g. Smith *et al.,* 2004). . For

509   example, during the drier late Pleistocene last glacial maximum, the body mass groups of

510   mammalian faunas in South America and Africa were quite similar. However, during the

511   wetter Holocene climatic optimum there was a decrease in open vegetation areas that lead

512   to the loss of larger-sized mammal lineages in South America, whilst they survived in

513   Africa. As a result, today Africa is richer in the number of species above 5 kg (De Vivo and

514   Carmignotto 2004). In addition, Louys *et al.,* (2011) hypothesise that faunal exchange over

515   the past several million years between Africa and Asia contributes to community

516   convergence, whereas the much longer separation of the New World from the Old World

517   relates to differences between their communities. Furthermore, they posit that historical

518   factors function on a much longer temporal scale in shaping community structure, which

519 suggests that some caution is warranted in selecting comparative communities from

520 across the world for palaeoecological reconstructions of sites located on a continent that

521 has been long separated from the others, or for analyses involving deep time. This can be

522 interpreted from our results, too. Although we did not analyse continental differences in the

523 other ecovariables, our results show only relatively small numbers of similar mammalian

524 community structures within worldwide tropical vegetation classes. This indicates that

525 historical and ecological factors are shaping mammalian community structure slightly

526 differently in relatively similar primary production environments. (Endler 1982).

527 In addition to caveats regarding the usefulness of body mass as a habitat discriminator,

528 our results provide an additional principal observation for palaeoecological community

529 studies. Some vegetation groups represent a continuum of cover (TMC-TBS-TRF, RGD-

530 SGW-MGS-SDS) that are, at least at the worldwide comparison, too detailed to

531 differentiate when broad generalities are sought. This may be related to the methodology,

532 in which habitats on this continuum are forced into discrete categories for the sake of

533 analysis. The ecological reality is that differences between these groups are probably

534 much more subtle than these discrete categories can be analysed using our ordination-

535 based approaches and other common tests. One way around this problem may be to

536 focus on reconstructing not habitat categories specifically, but the variable amount of

537 canopy cover available in them, as Louys, *et al.,* 2015 have done. However, one may seek

538 more ecological detail than this, whereby the use of well-defined habitat categories is both

539 convenient and analytically manageable. Where this option is pursued, we suggest using

540 three worldwide tropical major ecosystems: "Humid, closed forests" that contains TMC,

541 TBS, and TRF; "Seasonal or interrupted forests and grasslands" that contains RGD, SGW,

542 and STW; and "Seasonal, open drylands" that contains MGS, SDS, and TUN (TBC and

543 SWP were difficult to differentiate from the other groups so they are excluded from our

544   three groups; the former exists mostly in mid-latitudes and is a marginal habitat in the

545   Tropics, whilst the latter is a generalised category that can be found naturally within many

546   other habitats). These broad groups are similar in structure to those described by Mendoza

547   *et al.* (2004): "evergreen forests", "wooded savannahs that share grass and browse" and

548   "arid communities with sparse plant cover". They identified these in strictly African

549   communities, but they appear to hold at the global level, as well, further highlighting their

550   utility in ecological reconstructions. Interestingly, these authors do not consider locomotion

551   in their study, but assign each large mammal taxon to a group which combines feeding

552   strategy and body size.

553

554   The data as we have analysed them herein demonstrate their wide applicability in

555   distinguishing between modern habitats and, by extension, fossil localities where relatively

556   complete species lists can be obtained. We appreciate that defining palaeospecies is not a

557   straightforward task, but since we find that more precise habitat reconstructions are every

558   bit as possible as broad ecosystem discrimination where increasingly detailed species

559   information is analysed, palaeontological research should continue to approach questions

560   of individual species adaptive complexes, as well as palaeocommunity structures and

561   habitat affiliations.

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754

BIOSKETCH

756

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758   mammals and his main interest is linking current mammalian community structures with

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763   of fossil mammals in reconstructing the environment of hominin evolution.

764

SUPPORTING INFORMATION

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

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

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