Continent-wide Patterns in Mammal Community Structure: Diet, Locomotion, and Body Mass

Kari Lintulaakso [a], Kris Kovarovic [b]

[a] Finnish Museum of Natural History LUOMUS, Kumpula Manor, Jyrängöntie 2, Helsinki, 00014 Helsinki, Finland

[b] Department of Anthropology, Durham University, South Road, Durham DH1 3LE, UK

Abstract

We test if tropical vegetation categories in Africa, America and Asia can be differentiated by their mammal communities. We studied 163 localities assigned to Olson's (1983) vegetation categories in five ecosystems. Non-volant species over 500 g were classified into locomotion, body mass, and two hierarchical dietary groups and the resulting community structures were analyzed using NPMANOVA and SIMPER. Results show the community structures are significantly different between most of Olson's vegetation categories in Africa and America. In Asia, the differences are not significant, although there are a limited number of vegetation categories in our Asian dataset. In Africa, both diet variables are the best at differentiating the vegetation categories followed by locomotion. In America, diet 2 is the best variable followed by the others. Body mass was not a good discriminator in Africa, but is moderately good in America. Specific differences between the continents and reasons underlying these differences are discussed.

Keywords: community structure, continents, ecovariable, Olson (1983), NPMANOVA, SIMPER, tropics, vegetation

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1. Introduction

1.1 Mammals and community structure

Following their emergence in the early Jurassic or late Triassic, mammals quickly became established and rapidly diversified, adapting well to life alongside dinosaurs (Hu et al., 2005, Luo 2007, Luo et al., 2011, Luo et al., 2015, Grossnickle et al., 2019). Although the extinction of the dinosaurs opened up a multitude of niches for mammals to invade, their ability to do so successfully was underpinned by their pre-existing diversity. They had long since adapted to a variety of ecological conditions on the land, in the sea, and in the air – running, swimming, gliding, climbing, and digging just as they continue to do today (Hu et al., 2005, Ji et al., 2006, Luo 2007, Luo et al., 2011, Chen and Wilson 2015, Luo et al., 2015, Meng et al., 2015, Luo et al., 2017, Grossnickle et al., 2019).

The deep and successful evolutionary history of the mammalian class has resulted in an incredible amount of morphological and behavioral diversity across the globe. When viewed at a regional level, this diversity is also evident but, of course, the species composition of mammal communities in different areas is not the same. However, as described in a classic study by Andrews et al. (1979), when communities with different taxonomic compositions are found in similar sorts of environments, they express adaptive similarities that relate to their exploitation of the trophic and spatial niches available in their habitats.

When these dietary and locomotor ecovariables are viewed as a composite for a community, it is referred to as the “community structure”. It is often conceptualized as the number or relative proportion of species in a community that are adapted to broad types of diet (e.g. herbivore, carnivore, frugivore, etc.) or for locomotion in a particular spatial sphere (e.g. arboreal, terrestrial, aquatic, etc.). Body size is also often considered as part of community structure, as the size of an animal places limits on what resources and parts of a habitat it can or cannot exploit.

A significant body of research devoted to understanding how mammal communities are structured in different environments and associated methods for understanding this phenomenon has developed over the last several decades (see Kovarovic et al., 2018), much of it with a view to reconstructing past environments via an assessment of fossil community structure (Andrews et al., 1979, Nesbit Evans et al., 1981, Reed 1997, Reed 1998, Andrews and Humphrey 1999, Kovarovic et al., 2002, Su and Harrison 2007, Reed 2008, Croft et al., 2008, Su et al., 2009, Louys et al., 2011, Meloro and Kovarovic 2013, Catena and Croft 2020).

There are two fundamental data requirements underpinning this approach. Firstly, it is critical that we can properly assess the dietary and locomotor behaviors of fossil species. Although proxies such as stable isotopes are useful in this regard, it is largely through functional morphological and ecomorphological studies, underpinned by detailed work in comparative skeletal and dental morphology that we can understand the variety of solutions that mammals have evolved for exploiting different ecological niches. Secondly, community structure studies are reliant on thorough observations of the species at present day localities in a variety of habitats, and reliable assessments of the number of species in fossil communities at paleontological sites. Complete lists of species inhabiting well-defined areas are harder to acquire than one might expect. Species lists may have been compiled many decades ago, which in and of itself is not a negative (Boshoff and Kerley 2010), however it was sometimes the case that only medium and large mammals were recorded, but small-bodied mammals were neglected due to the time and expense of the methods required for observing them. Many of these historic localities' habitats have been lost or disrupted through human activity as well, so their communities can no longer be verified. For different reasons, fossil mammal communities may also present challenges, particularly those relating to the vagaries of the fossil record whereby each site's specific taphonomic history may result in the loss of portions of the community (particularly where smaller species are concerned), and the difficulty of identifying and defining unique species in the fossil record.

With respect to the data requirements for community structure analyses outlined above, it should be clear that large-scale, accessible databases containing information on modern and fossil mammals and species lists from both modern and fossil localities have become a necessity, acting as repositories of knowledge that can be shared, discussed, and studied. Although there are other large, publicly accessible databases that contribute to research in this area (for example, PanTHERIA for modern mammals (Jones et al., 2009), The Paleobiology Database and Neotoma (Uhen et al., 2013) for fossil taxa and Conservation Archive (Grace et al., 2019) for modern and fossil species), the NOW Database is particularly unique because it is the only global fossil database dedicated solely to mammals (The NOW Community 2021). It recognizes the importance of the ecovariables the others and we commonly incorporate into this community structure research, with fields for each species' body size, diet, and locomotion.

1.2 Patterns in mammal community structure

As noted, early work on mammal community structure demonstrated that irrespective of taxonomic composition and geographic location, mammal community structure is similar when the communities live in the same types of habitats. For example, tying together a consideration of both trophic and spatial niches, there is a widely acknowledged relationship between the number of frugivores and the number of terrestrial species, such that forested environments have a greater proportion of frugivorous species adapted for movement in the arboreal substrate in comparison to grazing species and large-bodied herbivores who locomote terrestrially (Bodmer 1990, Reed 1997, Louys et al., 2011). There are other known global generalities, including differences in community structure that vary according to latitude (Fleming 1973) and habitat complexity (August 1983).

Interested in further understanding mammal communities on a global scale, we previously evaluated how community structure differentiates between broad ecosystems and several tightly defined vegetation types (as described by Olson et al., 1983) in the tropics (Lintulaakso and Kovarovic 2016). We analyzed a large dataset of mammal species lists and ecovariable classifications associated with each taxon recorded at 169 locations on four continents (Africa, America, Asia and Australia), and found that ecosystems and vegetation categories can be clearly distinguished from one another, but that mammal diets and locomotion were more closely linked to habitat differences than body mass profiles. Along the lines of other findings using smaller datasets (Kay and Madden, 1997; Reed 1997, 1998; Louys et al., 2009; Kay et al., 2012), we observed that the number of frugivores, grazers and mixed feeders contributed to habitat differences, whilst arboreality and subterranean movement were the two most important locomotor adaptations.

These patterns point to some fundamental rules governing the structure of communities in certain habitat types, but the ecosystems on each continent have also followed a unique evolutionary pathway to result in their present-day communities (Olson 1966, Endler 1982, Janis 1993). In fact, grazing and browsing herbivores evolved from frugivorous mammals (Bodmer and Ward 2006) suggesting that community structure at some point in the past would not be directly comparable to communities in the modern world where the adaptations differentiating frugivores and from herbivores, grazers in particular, are so clear. Indeed, the issue of non-analog habitats and mammal communities is a line of inquiry in its own right (for example, Graham 2005, Soligo and Andrews 2005, Semken Jr et al., 2010, Faith et al., 2019).

A focus on global trends linking mammal communities and habitat is likely to obscure differences that exist both within and between continents due to historical differences in community evolution and assembly. In this chapter, we therefore investigate tropical mammal community structure in three large areas: Africa, Asia and the Americas (which we refer to as "America"). We use a slightly modified dataset from our earlier study (Lintulaakso and Kovarovic 2016); we exclude Australia, which had only four localities, and restrict our study to vegetation categories with two or more localities. The aims are to explore if global patterns in community structure hold at the level of the continent, to identify which ecovariables are responsible for differences between the continents' community structures, and discuss the factors underpinning observed differences.

2. Materials and Methods

2.1. Localities and species

This study includes 163 modern localities in the tropical zone between 23° 30′ N and 23° 30′ S (Fig. 7.1; see also Appendix S1 in Supporting Information of Lintulaakso and Kovarovic (2016)). We selected localities where the mammal communities are recorded as including 20 or more species, but there are some cases, such as tundra and montane habitats, where the natural number of species is not often this high. Thus, a handful of localities have relatively small species lists, but this is an accurate representation of their mammal communities and is not the result of poor sampling or biased observations of resident taxa. There are, in total, 538 unique species in our dataset. Following established practice, we do not include Chiroptera, Sirenia, and Cetacea, or any species weighing less than 500 g on account of inconsistencies in recording and reporting on their presence in modern habitats. Lists of species at each locality can also be found in Appendix S1 in the Supporting information of Lintulaakso and Kovarovic (2016).

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2.2. Vegetation categories

Vegetation was classified according to the “Major World Ecosystem Complexes Ranked by Carbon in Live Vegetation” GIS dataset, which organizes the Earth's land surface in 0.5 by 0.5-degree grid cells and classifies each grid according to the dominant type of vegetation cover (Olson et al., 1983, Olson, et al., 1985). This is a hierarchical system of classification; our analyses are conducted at the level corresponding to Olson et al.'s (1983) sixth level, which takes landscape, latitude, altitude, temperature, moisture and seasonality into account. We call this the ‘vegetation category’ (Table 7.1). Categories associated with agriculture and human activity, and categories represented by only one locality were excluded. We used 11 categories in total, but not all are present on each continent; there are nine in Africa, 10 in America and four in Asia (Table 7.1). Detailed descriptions of selected categories are found in Olson et al. (1983). The number of localities included in each vegetation category on each continent is summarized in Table 7.1.

PLACE TABLE 7.1 ABOUT HERE

2.3. Ecological variables

We assigned each species to broad categories in four ecological variables including body mass, locomotor pattern, and two dietary categories. Taxa were assigned to a body mass category based on median body weights for both males and females from several published sources. These categories are modified from 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). There are six locomotor groups, which we use to describe the substrate(s) in which the species most frequently moves (Reed 1998, Miljutin 2009): arboreal (A), arboreal–terrestrial (AT), subterranean (S), subterranean–terrestrial (ST), terrestrial (T) and terrestrial–aquatic (TA). Finally, food preferences are divided into two levels (Table 7.2). Diet level 1 represents the species' broadest category of feeding strategy: animalivorous, frugivorous and herbivorous (Miljutin, 2009). Diet level 2 follows that of Eisenberg (Eisenberg 1981) with some modifications: mixed-feeders are included in the herbivore group, and aerial insectivores and foliage-gleaning insectivores are combined into a single insectivore category. Where a species' locomotion or diet was described in multiple references, the most frequently cited locomotor or dietary preference was used. All classifications are summarized for each species in Appendix S2 in the Supporting information of Lintulaakso and Kovarovic (2016), which also lists the original data references.

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2.4 Analysis

The number of species in each ecovariable category at a locality (i.e. the community structure) was transformed by log2(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)). The transformation decreases the relative contribution of abundant versus rare species in the analysis. In addition, the Bray–Curtis distance matrix (Bray and Curtis 1957, Legendre and Legendre 1998) that was used in this study, is known to be sensitive to differences in absolute abundances. With the transformation, this effect is largely reduced (Anderson and Willis, 2003). The distance matrix was used in a non-parametric a priori test for community structure differences among and between vegetation categories using the permutational multivariate analysis of variance (NPMANOVA; Anderson 2001). A general NPMANOVA analysis among vegetation groups was performed to see if there are any differences in the community structure in each continent and, if so, a separate pairwise NPMANOVA between vegetation categories was conducted to identify which vegetation community structures were statistically dissimilar. This was followed by SIMPER (similarity percentage) analysis, which determines the relative contribution of each ecological variable to the dissimilarity between groups (Clarke 1993). A good discriminator is one that consistently contributes to both the within-group similarity and between group dissimilarity. In the SIMPER results, we only report the cumulative contribution up to 75%. Analyses were conducted in R 3.0.0, using R-packages stats and vegan (R Development Core Team 2005, Oksanen et al., 2007).

3. Results

The initial NPMANOVA results showed that the mammalian community structures are significantly different between all of the vegetation categories for each ecovariable in both Africa and America ($p < 0.001$, Table 7.3). In Asia, there were no significant differences found (Table 7.3). These results justified proceeding to the pairwise NPMANOVA and SIMPER analysis for Africa and America. However, they suggest that the vegetation categories cannot be distinguished based on the mammal communities in Asia, so follow-up tests are unnecessary. For exploratory reasons, we did continue with these analyses in Asia, but caution the use of the results to draw any major conclusions regarding this continent unless they can be verified with a much larger sample size. We had only 24 localities representing four vegetation categories, unlike Africa and America where a larger, more ecologically diverse sample was available (see Table 7.1).

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3.1 Africa ecovariable analyses

In Africa, the pairwise NPMANOVA results show that both diet variables are the best at differentiating the nine vegetation categories present (Table 7.4). 25 out of a possible 36 vegetation category pairs (69%) were significantly different at both diet level 1 and diet level 2, although the significant pairs themselves differed in a few instances between the levels. Locomotion was also a good ecovariable with 23 significantly different pairs (64%), while body mass performed poorly with only 13 (36%). Nine vegetation pairs out of 36 were not differentiated by any of the variables (25%).

In terms of mammal locomotion, SIMPER results indicate that the number of terrestrial, arboreal and subterranean–terrestrial species is important for the dissimilarities between communities; the arboreal–terrestrial, terrestrial–aquatic, and subterranean species contributed much less so (Table 7.4). For body mass, it is the number of smaller species in categories A, B, and C, which has the highest contribution to the dissimilarities between pairs, followed by the number of taxa in the highest mass category (360+ kg; (F) Table 7.4). Finally, all three of the diet level 1 categories contribute to vegetation category dissimilarities, whilst at diet level 2 the carnivores, grazers, frugivore–granivores, frugivore–herbivores and browsers are the most important (Table 7.4).

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3.2 America ecovariable analyses

In America, the pairwise NPMANOVA results show that diet level 2 is the best ecovariable for differentiating the vegetation category pairs, with 25 out of a possible 45 pairs (56%) being significantly different. The other three variables performed similarly; body mass differentiated 23 pairs (51%), Diet Level 1 differentiated 22 pairs (49%), and locomotion differentiated 21 pairs (47%). 36% of the pairs, 16 out of the 45, were not differentiated by any of the ecovariables (Table 7.5).

SIMPER results indicate that the number of arboreal, terrestrial and arboreal–terrestrial species is important for the dissimilarities between communities; the subterranean–terrestrial, terrestrial–aquatic, and subterranean species contributed much less so (Table 7.5). In terms of body mass, the number of small species in categories A and B has the highest contribution to the dissimilarities between pairs (Table 7.5). Finally, the number of frugivorous and animalivorous species is important at diet level 1, and at diet level 2 frugivore–granivores, carnivores, frugivore–omnivores, frugivore–herbivores and insectivores contribute most to the dissimilarities between communities (Table 7.5).

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3.3 Asia ecovariable analyses

As noted above, in Asia small sample sizes restricted the number of analyses we could perform with the mammal communities, as only four of the vegetation categories in two major ecosystems are represented by the localities we included on this continent (see Table 7.6). Although the among-vegetation category NPMANOVA results were poor for Asia, yielding no significant differences (Table 7), we proceeded with further exploratory analyses. Interestingly, we do find that while the pairwise NPMANOVA does not identify any significantly different vegetation category pairs in diet level 1 and locomotion (they are therefore not included in Table 7.6), body mass differentiates two out of six vegetation category pairs and diet level 2 differentiates one pair (Table 7.6).

SIMPER indicates that the number of small species in categories A and B provides the highest contribution to the dissimilarities between group pairs (Table 7.6). For diet level 2, SIMPER shows that the number of carnivores, frugivore–granivores, frugivore–herbivores, insectivores and browsers at diet level 2 contribute most to the dissimilarities between communities (Table 7.6).

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4. Discussion

Each continent studied has a different array of vegetation categories present. We firstly discuss which of these categories are distinguishable from the others on each continent, grouping them according to the five major ecosystems (Table 7.1) and focusing on the broad patterns observable in our results recognizing, of course, that there is certainly scope to further plumb the results for more nuanced comparisons within both individual ecosystems and continents. Secondly, we consider the underlying reasons for our data being able to distinguish between vegetation categories from the perspective of mammalian adaptations on each continent. Thirdly, we discuss some of the reasons that mammal communities differ between the continents.

4.1 Africa

The two diet variables were the best discriminators of the nine vegetation categories present in Africa, followed closely by locomotion (Table 7.4); they distinguished between vegetation categories in approximately 2/3 of the cases. Body mass was only successful in 1/3 of the cases, and therefore it cannot be considered a particularly good discriminator of vegetation categories on this continent.

Generally, the three vegetation categories belonging to the major forest and woodland ecosystem (FW) were distinguishable from all of the others based on all or some of the community structure variables. In the interrupted woods (IW) ecosystem, only the tropical montane complex (TMC) can be easily distinguished from other vegetation categories. The remaining two categories, succulent and thorn woods and scrub (STW) and tropical savanna and woodlands (SGW), were less consistently distinguishable from categories in the other ecosystems, except for the pairing of desert and semidesert (SDS) and tropical savanna and woodlands (SGW), which could be told apart based on both locomotion and diet level 1.

Warm or hot shrub and grassland (MGS) is significantly different from the three forest and woodland (FW) categories, tropical montane complexes (TMC), and desert and semidesert (SDS) in almost all cases. It cannot be told apart from the other interrupted woods (IW) categories or wetlands, swamp and marsh.

Desert and semidesert (SDS) differs from the forest and woodland (FW) categories in all but one case, where body mass cannot differentiate between it and equatorial rain forest (TRF). It is not easily told apart from interrupted wood (IW) (except for tropical savanna and woodlands (SGW) on the basis of locomotion and diet level 1 as noted above, and from tropical montane complexes (TMC) on the basis of diet level 2). It is interesting that it does not clearly differentiate from the interrupted wood category succulent and thorn woods and shrub (STW) in any analysis, as this category possesses much greater amount of tree cover than a desert or semidesert habitat. It can usually be distinguished from warm or hot shrub or grassland (MGS), but never from wetlands, swamp and marsh (SWP).

The wetlands, swamp and marsh category (SWP) is not distinguishable from any others with respect to body mass. The other three ecovariables are good discriminators, but only in a limited number of cases: the forest and woodland categories tropical/subtropical broad-leaved humid forest (TBS) and equatorial rain forest (TRF) and the tropical montane complexes (TMC).

4.2 America

There are ten vegetation categories in America representing a range broadly similar to that found in Africa. The ecovariables were moderate discriminators, distinguishing between 47% and 56% of the available pairs of vegetation categories (Table 7.5). This includes body mass, which was not as useful in telling them apart in Africa. Nonetheless, fewer vegetation pairs overall can be distinguished on this continent compared to Africa, so generalized patterns are more difficult to discern.

In America, the forest and woodlands (FW) ecosystem has four vegetation groups; equatorial rain forest (TRF) is distinguishable from all of the other vegetation categories based on all four ecovariables. Tropical/subtropical broad-leaved humid forest (TBS) is nearly as successfully distinguished in all but a few vegetation pairs; most notably the interrupted woods category tropical montane complexes (TMC). The remaining two forest and woodlands (FW) categories often can’t be told apart from anything else, except for other categories within the same ecosystem and, where tropical dry forest and woodland (RGS) is concerned, from both grass and shrub complexes (MGS) and tundra (TUN) across all ecovariables.

In interrupted woods (IW) the first thing that stands out is the inability of the mammal communities to distinguish tropical savanna and grasslands (SGW) from any other category, with the exception of tropical/subtropical broad-leaved humid forest (TBS) and equatorial rain forest (TRF), and a couple of other isolated pairs, across all ecovariables. The other two interrupted wood (IW) categories behaved quite differently; succulent thorn woods and shrub (STW) could frequently be distinguished from the others, *except* for those in the same ecosystem, whilst tropical montane complexes (TMC) could generally only be distinguished from warm or hot shrub and grassland (MGS) and tundra (TUN).

Warm or hot shrub or grassland (MGS) differs from most of the vegetation categories, except for deciduous forests, warm woods with conifers (TBC), tundra (TUN), and warm or hot wetlands, swamp/marsh (SWP). It can only be told apart from tropical savanna and woodlands (SGW) based on body mass. Tundra (TUN) generally differs from the same vegetation categories as warm or hot shrub or grassland (MGS) based on the same ecovariables, with a few minor differences.

Warm or hot wetlands, swamp/marsh (SWP) does not differ from most of the other vegetation categories. However, as noted in Africa as well, it is distinguishable from equatorial rain forest (TRF). It can also be distinguished from succulent and thorn woods and shrub (STW) where locomotion is concerned, and from tropical/subtropical broad-leaved humid forest (TBS) based on diet level 1.

4.3 Asia

There were only four vegetation categories represented by our Asian sample of localities, and only body mass and diet level 2 yielded any significant differences between the vegetation pairs (Table 7.6).

Three of the four vegetation categories belong to the forest and woodlands (FW) ecosystem. Tropical dry forest and woodland (RGD) cannot be distinguished from any other category. Conversely, equatorial rain forest (TRF) can be told apart from tropical/subtropical broad-leaved humid forest (TBS) based on both ecovariables. Tropical montane complexes (TMC), the only category from the interrupted woods (IW) ecosystem can also be distinguished from equatorial rain forest (TRF), but only based on body mass. Although few conclusions can be drawn from the limited Asian results on their own, we note that forest and woodland (FW) vegetation categories tend to be easily distinguished from others in both Africa and America, particularly equatorial rain forest (TRF), which is reflected here in Asia, as well.

4.4 Mammal ecovariables

Our focus now is largely on Africa and America where the sample sizes were more robust and thus observations are better substantiated. However, we bring Asia into the discussion where relevant.

The types of vegetation present on Africa and America are quite similar with a few key differences: in America, deciduous forests and warm woods with conifers are present in the forest and woodlands ecosystem, and tundra replaces desert and semi deserts. Despite similarities in vegetation, and some generalities that have been described above, the set of ecovariables responsible for telling apart the categories, and the groups of mammals within them, differ somewhat between the continents.

Firstly, body mass is, out of all of the ecovariables, the worst at differentiating between vegetation categories. In Africa, it can only differentiate between 36% of the vegetation pairs, but it performs much better in America where it can tell 50% of them apart. On all of the continents the number of smaller species weighing up to 45 kg (categories A and B) make the highest contribution to the dissimilarities identified in SIMPER, while in Africa two additional body mass groups, 45–90 kg (C) and 360+ kg (F), are required to have a cumulative contribution to dissimilarities over 75%.

On a global scale, body mass is a poor discriminator, and we have previously recommended against its use as an ecovariable in large-scale studies (Lintulaakso and Kovarovic 2016). However, body size distributions on each continent do in fact differ, with Africa having a higher proportion of larger species than either Asia or America. On a smaller scale, this variable may be more useful (Brown and Maurer 1989), which we see some evidence for in our results. In America, for example, it is in fact useful for distinguishing the two most moist and complex forest types (tropical/subtropical broad leaved humid forest, TBS and equatorial rain forest, TRF), as well as the two most open vegetation categories, tundra (TUN) and shrub and grassland (MGS), from others. The smaller species allow equatorial rain forest (TRF) to be distinguished from other vegetation types in Asia, as well. In Africa, body mass is able to distinguish some of the forest and woodland categories from the others, with no consistent pattern, yet it is the only ecovariable differentiating tropical dry forest and woodland (RGD) from succulent and thorn woods and shrub (SGW). So, while it appears that body size may have some utility in differentiating multiple vegetation types in America, and possibly Asia, it should be used with caution and in only specific cases in Africa. (Lintulaakso and Kovarovic 2016).

Diet and locomotion show some interesting differences between the continents, as well. Both in Africa and America, the number of terrestrial and arboreal species separate the vegetation categories, but in a different order in the cumulative contribution in SIMPER. In Africa, the number of terrestrial species contributes more than the number of arboreal species, while in America the order is reversed. Subterranean-terrestrial species had the third highest contribution in Africa, while in America it was the number of arboreal-terrestrial species. The importance of terrestrial and arboreal species has been reported in other studies (Reed 1997, Reed 1998, Louys et al., 2011). The role of subterranean-terrestrial species in Africa may relate to the presence of significant dry and wet seasons, as hiding underground has been shown to be one of the mechanisms to survive seasonal fluctuations (Liow et al., 2009). The lack of arboreal or arboreal-terrestrial species in some of the American vegetation categories clearly show the absence of tree cover, as in the case with the differentiation of tropical montane complexes (TMC) from tundra (TUN) where the number of arboreal-terrestrial species (AT) is the greatest contributor to their differences.

Quite often in palaeoenvironmental reconstructions, the focus is on large-bodied, herbivorous species to the exclusion of small mammals (Janis et al., 2004, Soligo and Andrews 2005, Eronen et al., 2010, Damuth and Janis 2011, Saarinen 2014). We do note that both grazers (G) and browsers (B) are important in Africa but not in America, and mixed-feeders (MF) contribute little to the differences regardless of the continent. Despite the frequent focus on the herbivore guild, our full community approach shows that with respect to diet level 1 in Africa and America, it is actually the number of frugivorous species, which has the highest cumulative contribution to dissimilarities between the categories. This is followed by the number of herbivores and animalivores in Africa, and animalivores in America. The importance of herbivores in Africa in differentiating the vegetation categories is perhaps expected, as this continent is well known for its diverse herbivorous fauna, while tropical America is not (Owen-Smith 2013). The role of animalivores in palaeoenvironmental reconstructions is often overlooked (but see Belmaker 2018), but our diet level 2 results show that they are meaningful in a community approach; the importance of animalivores (including carnivores, C, and insectivores, I) is high. In Africa, carnivores have the highest cumulative contribution to dissimilarities between the vegetation categories, and in America, they contribute the second highest. This is also supported by the results for Asia in which carnivores have the highest contribution to dissimilarities (although only one vegetation category pair can be differentiated).

In addition to these differences in the mammal communities and what they are responsible for on each continent with respect to distinguishing between vegetation categories, we make a few additional observations in light of our previous study on global patterns (Lintulaakso and Kovarovic 2016). Firstly, warm or hot wetlands, swamp/marsh (SWP) did not differentiate globally except from some forests and extremely open categories, but we find that there are differences between the continents. In America, it can only be consistently told apart from equatorial rain forest (TRF) based on the number of small-bodied, arboreal, or frugivorous taxa, but in Africa, it is distinguishable from equatorial rain forest (TRF) as well as broad leaved humid forest (TBS) and tropical montane complexes (TMC), usually based on terrestrial species and frugivores. Notably, the number of terrestrial-aquatic species does not contribute to any of the distinguishable vegetation category pairs. Wetlands and swamps are distributed throughout many different habitat types and are associated with a diversity of vegetation, forming when water levels are consistently high and drainage is low, and while they are often associated with rivers or lakes, they may also form outside of these hydrological conditions. They likely capture certain aspects of mammal communities that are adapted for the variety of non-swamp habitats that can flank these areas, making swamps and wetlands difficult to differentiate (Lintulaakso and Kovarovic 2016).

Secondly, where vegetation categories can only be distinguished from some forest and woodlands (FW) on a global level they are also frequently distinguishable from tropical montane complexes (TMC) as well, although this vegetation is grouped under interrupted woods (IW) on account of its lower mean carbon density (Olson et al., 1983). This suggests that although the tropical montane vegetation is different from those of true forests, the mammal communities that have adapted to its available niches do not differ completely from forest community structures, particularly deciduous forest, warm woods with conifers (TBC) and tropical/subtropical broad-leaved humid forest (TBS) (Lintulaakso and Kovarovic 2016). On a continent scale, the situation is quite different, however. In Africa, tropical montane complexes (TMC) are consistently different from the other categories, which is related to the number of terrestrial species in most cases, although there is no clear pattern in diet. In America, this category can only be told apart from vegetation complexes at either end of the spectrum of complex and woody cover: equatorial rain forest (TRF) on the one hand, and warm or hot shrub and grassland (MGS) and tundra (TUN) on the other. It appears that in America there is a greater overlap between communities in the forest and woodlands and interrupted woods groups.

Finally, we also previously observed how tropical savanna and woodlands (SGW) could not be differentiated from tropical dry forest and woodland (RGD) or warm or hot shrub or grassland (MGS) on the basis of any ecovariable on a global scale (Lintulaakso and Kovarovic 2016). Although some ecovariables were occasionally successful at differentiating it from other vegetation categories we noted the failure of the mammal communities to tell SGW apart from

RGD and MGS because these three categories are in quite different ecosystems – forest and woodlands (FW), interrupted woods (IW), and grass and shrub complexes (GS), and therefore possess different amounts of woody growth that should presumably support very different types of species. Looking at Africa and America separately, this global pattern holds in all but two cases; fewer small species (A) differentiates it from RGD in Africa and a greater number of small species (A) from MGS in America. It is curious that neither locomotion or diet play a role in these differences, but these are both good examples of where body mass profiles can be successfully used in specific cases.

4.5 Continental differences – history matters

What we have shown in this chapter is that global patterns in mammal community structure do not always hold at continental level. Where an ecovariable may be only marginally successful at differentiating vegetation categories globally, it can be more useful on some continents or in specific cases where only certain vegetation types are being considered. The continents differ taxonomically in their mammal communities, but why might they differ in community structure when comparing vegetation types that theoretically present similar niches to be filled? The ecosystems and resident species on each continent have evolved over long periods of time, experiencing unique historical pathways to reach their present-day forms. In short, both ecology *and* history matter (Endler 1982).

The global pool of species has had millions of years to evolve compared to continents, smaller regions therein, or local communities, all of which represent different spatial and temporal scales (Rapacciuolo and Blois 2019). Global-scale patterns in community diversity may be said to represent the top level of a hierarchy; they are relatively stable because they have evolved over extremely long periods of time and are rather unaffected by smaller scale changes to community structure. The observation that the tropical forest ecosystem is distinguishable from tropical tundra, deserts, and grassland (Lintulaakso and Kovarovic 2016) suggests both that mammals have been adapting to the very different niches presented by these ecosystems over the long term and that there is little functional overlap in how animals can successfully exploit them.

Differences in how mammal communities can be used to tell apart vegetation categories within broad ecosystems are observable at smaller scales, such as continents as we have done in this chapter. Continental species pools evolve over thousands to millions of years, resulting in some differences; for example, South American mammals were largely separated from North American communities until the Great American Biotic Interchange (GABI) began when the land bridge between the two started to emerge and finally completed formation. This led to waves of dispersal between the continents that resulted in many changes to mammal communities on either side of the previous divide (see Woodburne 2010). The scenario is quite different elsewhere in the world, where Africa, Europe and Asia were separated in deep time (Rage and Gheerbrant 2020) but have since been in contact so that faunal exchange has facilitated some aspects of community convergence, particularly during the last few million years (Louys et al., 2011). Mammalian body mass profiles provide another good example of continent scale differences. The dominance of large bodied taxa in Africa, which can be observed even in the Pleistocene fossil record (Janis 1993, De Vivo and Carmignotto 2004, Louys et al., 2011, Fortelius 2013, Owen-Smith 2013), is in contrast to the higher proportion of smaller species present in America, with Asia falling somewhere in the middle (Lintulaakso and Kovarovic 2016). Differences in body mass distributions between the continents likely account for the difficulty of using body mass as an ecovariable in distinguishing habitats globally.

Regional species pools also differ; their number and character vary by continent (Lintulaakso et al., 2019). It is from these regional pools, which arise over tens to hundreds of years that local mammal communities, comprised of co-occurring species capable of interacting, are formed. This is the level of locality data in community structure analyses – species lists record these communities, which are the result of millions of years of evolution at different spatial and temporal scales and a number of different mechanisms. Articulated clearly by Vellend (2010, 2016), dispersal, drift, selection, and speciation are the four main processes responsible for the differences we see in communities across the globe. To this list we explicitly add a fifth mechanism: extinction, which can have long-term ecological and evolutionary impacts that translate into observable differences in community structure (Galetti et al., 2017).

The differences between African and American mammal communities that we report on in this chapter can be used to illustrate the impact of some of these mechanisms. At the end of the Quaternary, many of the world's megafauna went extinct. It is difficult to piece together a fine-grained chronology of these extinctions that would allow us to test hypotheses for specific drivers (usually posited as climate change or human impact or some combination of the two) (Barnosky and Lindsey 2010; Stuart 2015), but regardless the outcome was profound. Although extinctions took place on other continents, North and South America in particular suffered the loss of its large-bodied mammals. In North America 70% of species weighing over 45kg went extinct and South America lost 80% of its genera overall; contrast this to Africa where the majority of its large mammals survived including elephants, giraffe, rhinoceros, hippopotamus, zebra, and a multitude of others (Koch and Barnosky 2006; Stuart 2015). Even earlier than the late Quaternary extinctions, large-scale dispersals and subsequent selection had a significant impact on the resultant communities in Africa, Eurasia and the Americas. As noted above, Africa, Europe, and Asia have been in contact for quite some time. Dispersals of adaptable or otherwise already well-suited groups of mammals over long and short periods of time between these continents has resulted in some faunal similarities that depend on the timescale considered. For example, members of the order Proboscidea migrated out of Africa during the late Oligocene (Antoine et al., 2003) and their ancestors quickly and successfully colonized Asia, Europe, and eventually both North and South America. So, at some point in the past five continents hosted these large bodied herbivores, but in more recent times they have gone extinct from all but Asia and Africa (Sanders et al 2010). Another example is the significant impact of GABI on the fauna following a very long period of separation between American landforms. The carnivore guild in South America prior to GABI exhibited quite low taxonomic diversity which increased with the arrival of placental carnivorans from the North (Croft 2006). Additionally, endemic South American species weighing over 100 kg were lost during the Quaternary following the interchange (Fariña et al., 2013), including during the recent Holocene climatic optimum that resulted in the loss of open vegetation habitats favored by larger species, from which they were unable to recover (De Vivo and Carmignotto, 2004). South America in fact once hosted a very high proportion of large-bodied mammals that was similar to that seen in Africa, but they had also adapted differently to the available trophic niches such that only 40% of Pleistocene South American herbivores weighing over 100 kg were grazers, compared to 70% in Africa where a much more distinct separation between grazing and browsing ungulates evolved (Owen-Smith 2013). Generally, following the GABI, North American species were more successful in their new southern environments, whilst few southern species were able to adapt well to novel northern niches. Many differences between North and South American mammal communities have their roots in the GABI and events afterwards. Our analysis will not identify these clearly, as we included both continents in our consideration of “America" in the tropics, but one general pattern that we can identify is the relatively larger proportion of small mammals and their importance in distinguishing between some forest vegetation categories from others (Fariña et al., 2013).

What might the combined influence of ecology and history mean for mammal community structure based research, particularly where paleoecological reconstructions are sought? Their impact is important to the decision regarding the nature of the modern community dataset against which paleolocalities are assessed. Is a global comparative dataset always useful or might there be cases where it is arguably better to include only communities from within the same continent or region as the focal locality? It goes without saying that the final choice rests on the research question, but there are certainly grounds for limiting the modern sample of communities to specific locations, as well as selecting particular ecovariables and categories within them according to what is known about how they are capable of distinguishing between habitats in certain circumstances (Lintulaakso and Kovarovic 2016; Kovarovic et al 2018). This issue was approached by Croft et al. (2018) and Catena and Croft (2020) explicitly for South American fauna, finding that modern communities are poor analogues of ancient ones, following the significant changes that occurred because of GABI. This suggests that a global comparative dataset may be more relevant in studies of South American paleolocalities that predate GABI.

4.6 NOW and future paleoecological community structure research

The study described in this chapter is based on modern mammal communities; their usefulness in identifying differences in vegetation associations on multiple continents has been demonstrated here and elsewhere (Andrews et al., 1979, Andrews and Humphrey 1999, Louys et al., 2009). As we discussed, it follows that ecological reconstructions of fossil localities can also be accomplished through a similarly detailed understanding of the body mass, locomotion, and trophic adaptations of the constituent species of a paleocommunity. Researchers should therefore not relax efforts to develop ever more sensitive methods for identifying mammalian adaptations and assessing paleocommunity structure. An equally important endeavor in this area of research is increasing the accessibility of comprehensive datasets recording fossil mammal data from around the world. There are clear benefits to an active data repository such as the NOW database (The NOW Community 2021) – from allowing scholars to increase sample sizes, to verifying interpretations with those of other experts in the field, to preventing the maintenance of regional silos of scientific thought and activity. NOW contains a great deal of data that will benefit our knowledge of the past and promote collaboration.

Although a major aspect of our research involves using modern mammal community structure data to explore patterns on both global and regional scales, as paleoecologists we are interested in how this knowledge can be projected into the past. As something of a thought experiment, we asked if the NOW database would allow us to extend the analysis reported in this chapter to multiple fossil localities on the same continents. NOW recognizes the importance of the ecovariables we and others commonly incorporate into this form of research, with fields for each species' body size, diet, and locomotion, and it also covers paleo-localities across (but not restricted to) Africa, America and Asia. How many sites currently available in NOW meet our criteria for inclusion and contain the ecovariable data necessary for a mammal structure analysis?

At present, 6224 localities in NOW are set for public usage. Of these, 6166 possess mammal taxa in the relevant orders (we excluded Chiroptera, Sirenia and Cetacea) and which are over 500 g (however, we are not able to exclude all taxa weighing less than 500 g from these statistics because of the lack of body mass information for many taxa in the database). Out of the 6166 possible localities, 702 are within the tropical belt but only 140 of these have 20 or more taxa recorded. They are unequally distributed across the continents, with 110 located in Africa, 23 in Asia, and only 7 in (South) America.

A locality sample size of 140 is excellent, and not dissimilar to the sample of 163 (Table 7.1) we used in our study of modern communities, but the paleolocalities are skewed towards Africa which would make continent comparisons challenging (note that we also did not consider the geological age of the paleolocalities, which would of course be a major consideration in a fossil study). More problematic, a great deal of ecovariable data is missing. None of the communities are complete where body mass is concerned. Our locomotion categories are most similar to NOW's "Locomotion 2" field which describes the specific substrate in which terrestrial locomotion occurs, but none of the 140 communities had a full set of data here, either. We also matched our diet level 1 ecovariable against NOW's "Diet 1", which designates each species as a consumer of either animals or plants, or a mixed category called omnivore, and our more fine-grained diet level 2 ecovariable against NOW's equally detailed "Diet 3". Only two localities in Africa presented a full community dataset for Diet 3. In sum, none of the sites in NOW both meet our inclusion criteria and have a full complement of ecovariable data.

We also looked at how many sites had at least 50% of their species classified for each ecovariable to get a sense of "how close" they were to being completed for use in our study. The picture here is promising. Just over half of the African (n=66) and Asian (n=12) localities did have an average body mass associated with more than 50% of their taxa, three-quarters with diet level 1 (89 in Africa, 19 in Asia), and 16 with locomotion (all in Africa). There are also many other types of data included within NOW, some of which can be used to inform our work.

Average lengths and dental measurements can be used in regressions to predict body mass, for example.

The implication of the missing ecovariable classifications for many species in our 140 target localities in the database is clear: at present tropical paleo-mammal community structure cannot be investigated at the same scale as our modern community analysis. We do not, however, see this as a problem, but a sign of the currently unrealized potential of NOW to support work in investigating patterns of community structure and subsequent inferences about vegetation in the past. The database fields have been developed to allow meaningful ecological work across multiple continents, covering the entirety of the Cenozoic, and these fields are being populated at pace. Updates to species entries are particularly critical.

The scientific value of a resource of this nature should not be underestimated. We live in a time where both modern habitat loss and extinctions are occurring at an alarming rate; records of the mammals resident in many parts of the world are becoming historic documents. The fossil record, however, is where we stand to gain the most knowledge of mammal evolution, variation and adaptation, and a database such as NOW is where we must store and organize our understanding of this diverse class.

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TABLES

Table 7.1. The tropical Olson et al. (1983) major ecosystems and vegetation categories used in this study and the number of localities used in the analyses. AF = Africa, AM = America, AS = Asia. Modified from Lintulaakso and Kovarovic, 2016.

Major ecosystem	Code	Description of the vegetation category	AF	AM	AS
Forest and woodlands (FW)	TBC	Deciduous forests, warm woods with conifers		3	
	RGD	Tropical dry forest and woodland	16	3	2
	TBS	Tropical/subtropical broad-leaved humid forest	11	16	8
	TRF	Equatorial rain forest	7	17	12
Interrupted woods (IW)	STW	Succulent and thorn woods and shrub	4	8	
	SGW	Tropical savanna and woodlands	12	3	
	TMC	Tropical montane complexes	7	7	2
Grass and shrub complexes (GS)	MGS	Warm or hot shrub and grassland	11	4	
Tundra and desert (TD)	SDS	Desert and semidesert (no winter snow)	2		
	TUN	Tundra		2	
Major wetlands (WL)	SWP	Warm or hot wetlands, swamp/marsh	4	2	
Total:			**74**	**65**	**24**

Table 7.2. Dietary categories used in this study (Eisenberg, 1981; Miljutin, 2009). Modified from Lintulaakso and Kovarovic (2016).

Diet Level 1	Diet Level 2
Animalivore (A)	Carnivore (C)
	Piscivore (P)
	Myrmecophage (M)
	Insectivore (I)
	Insectivore–Omnivore (IO)
Frugivore (F)	Frugivore–Granivore (FG)
	Frugivore–Herbivore (FH)
	Frugivore–Omnivore (FO)
	Gummivore (U)
Herbivore (H)	Grazer (G)
	Mixed-Feeder (MF)
	Browser (B)

Table 7.3 The nonparametric multivariate analysis of variance (NPMANOVA, 9999 permutations, Bray-Curtis distance) of different Olson et al. (1983) vegetation categories within tropical Africa, America and Asia.

	Africa			**America**			**Asia**		
Variable	**df**	**F**	**p**	**df**	**F**	**P**	**df**	**F**	**p**
Locomotion	8,66	8.32	0.0001	9,56	10.85	0.0001	2,22	0.89	0.5095
Mass	8,66	4.08	0.0001	9,56	6.28	0.0001	2,22	2.37	0.0653
Diet level 1	8,66	8.88	0.0001	9,56	11.27	0.0001	2,22	1.24	0.2977
Diet level 2	8,66	6.85	0.0001	9,56	7.20	0.0001	2,22	1.76	0.1095

Table 7.4

Combined pairwise NPMANOVA and SIMPER results for African tropical mammal communities grouped by vegetation categories (Olson et al., 1983). Numeric values represent the average numbers of species in the analyzed vegetation categories. The asterisks represent statistically significant NPMANOVA results (*p<0.05; **p<0.01; ***p<0.001). Ecovariable categories in the top left of each individual table are those, which contributed to the differences between vegetation category pairs; the shading of the asterisks indicates which ecovariable is responsible for the highest contribution to the differences between two vegetation categories (SIMPER). Major ecosystem: FW=Forest and woodlands, IW=Interrupted woods, GS=Grass and shrub complexes, TD=Tundra and desert, WL=Major wetlands. Vegetation: RGD = tropical dry forest and woodland, TBS = tropical/subtropical broad-leaved humid forest, TRF = equatorial rain forest, STW = succulent and thorn woods and shrub, SGW = tropical savanna and woodlands, TMC = tropical montane complexes, MGS = warm or hot shrub and grassland, SDS = desert and semidesert (no winter snow), SWP = warm or hot wetlands, swamp/marsh; Locomotion: T = terrestrial, A = arboreal, ST = subterranean–terrestrial; Body Mass categories: A = 0.5–8 kg, B = 8–45 kg, C = 45-90 kg, F = 360+ kg; Diet Level 1: F = frugivore, H = herbivore, A = animalivore; Diet Level 2: C = carnivore , G = grazer, FG = frugivore–granivore, FH = frugivore–herbivore, B = browse

Locomotion					FW		IW			GS	TD	WL
					TBS	TRF	STW	SGW	TMC	MGS	SDS	SWP
		T			18.0	15.9	30.5	27.5	15.4	29.4	17.0	23.0
			A		9.9	13.0	1.0	2.7	7.4	2.3	0.0	3.3
				ST	3.5	3.1	6.3	5.0	2.4	4.4	3.0	4.3
FW	RGD	28.1	2.6	4.2	***	***	***	-	***	*	**	-
	TBS	18.0	9.9	3.5		-	***	***	**	***	*	**
	TRF	15.9	13.0	3.1			***	***	**	**	*	**
IW	STW	30.5	1.0	6.3				-	***	-	-	-
	SGW	27.5	2.7	5.0					***	-	*	-
	TMC	15.4	7.4	2.4						***	-	**
GS	MGS	29.4	2.3	4.4							-	-
TD	SDS	17.0	0.0	3.0								-

Body Mass					FW		IW			GS	TD	WL
					TBS	TRF	STW	SGW	TMC	MGS	SDS	SWP
	A				20.4	23.9	12.8	14.8	15.1	14.3	7.5	14.5
		B			10.6	10.7	14.5	12.8	10.0	13.8	9.0	10.0
			C		4.3	3.7	7.3	5.5	3.1	5.7	3.0	6.0
				F	3.4	2.4	4.8	3.6	2.7	4.0	0.5	3.0
RGD	13.8	11.6	7.3	4.2	***	***	-	*	***	-	**	-
TBS	20.4	10.6	4.3	3.4		-	**	-	-	**	**	-
TRF	23.9	10.7	3.7	2.4			**	-	-	***	-	-
STW	12.8	14.5	7.3	4.8				-	**	-	-	-
SGW	14.8	12.8	5.5	3.6					-	-	-	-
TMC	15.1	10.0	3.1	2.7						***	-	-
MGS	14.3	13.8	5.7	4.0							*	-
SDS	7.5	9.0	3.0	0.5								-

Diet 1					TBS	TRF	STW	SGW	TMC	MGS	SDS	SWP
		F			18.5	22.7	6.0	9.7	14.3	7.7	3.5	7.5
			H		9.5	7.1	19.5	15.5	8.0	17.4	8.0	13.0
				A	13.1	12.7	19.3	16.3	10.6	17.9	11.0	16.5
FW	RGD	8.4	17.4	16.5	***	***	***	-	***	*	**	-
	TBS	18.5	9.5	13.1		*	***	***	*	***	*	**
	TRF	22.7	7.1	12.7			***	***	-	***	*	**
IW	STW	6.0	19.5	19.3				-	***	-	-	-
	SGW	9.7	15.5	16.3					**	-	*	-
	TMC	14.3	8.0	10.6						***	*	*
GS	MGS	7.7	17.4	17.9							*	-
TD	SDS	3.5	8.0	11.0								-

Diet 2						TBS	TRF	STW	SGW	TMC	MGS	SDS	SWP
	C					10.8	8.9	15.8	14.3	9.0	15.3	9.5	13.8
		G				3.9	2.4	10.8	8.5	2.0	8.6	2.5	7.8
			FG			7.3	10.9	0.8	1.7	5.1	1.2	0.0	2.8
				FH		8.7	9.9	4.3	6.6	6.9	5.6	2.5	4.0
					B	4.0	3.6	6.5	4.8	4.3	6.0	3.0	4.0
RGD	14.9	10.6	0.8	5.3	5.7	***	***	***	-	***	**	**	-
TBS	10.8	3.9	7.3	8.7	4.0		*	***	**	*	***	**	**
TRF	8.9	2.4	10.9	9.9	3.6			***	***	**	***	*	**
STW	15.8	10.8	0.8	4.3	6.5				-	***	-	-	-
SGW	14.3	8.5	1.7	6.6	4.8					**	-	-	-
TMC	9.0	2.0	5.1	6.9	4.3						***	*	*
MGS	15.3	8.6	1.2	5.6	6.0							*	-
SDS	9.5	2.5	0.0	2.5	3.0								-

Table 7.5.

Combined pairwise NPMANOVA and SIMPER results for American tropical mammal communities grouped by vegetation categories (Olson et al., 1983). Numeric values represent the average numbers of species in the analyzed vegetation categories. The asterisks represent statistically significant NPMANOVA results (*p<0.05; **p<0.01; ***p<0.001). Ecovariable categories in the top left of each individual table are those, which contributed to the differences between vegetation category pairs; the shading of the asterisks indicates which ecovariable is responsible for the highest contribution to the differences between two vegetation categories (SIMPER). Major ecosystem: FW=Forest and woodlands, IW=Interrupted woods, GS=Grass and shrub complexes, TD=Tundra and desert, WL=Major wetlands. Vegetation: TBC = Deciduous forests, warm woods with conifers, RGD = tropical dry forest and woodland, TBS = tropical/subtropical broad-leaved humid forest, TRF = equatorial rain forest, STW = succulent and thorn woods and shrub, SGW = tropical savanna and woodlands, TMC = tropical montane complexes, MGS = warm or hot shrub and grassland, TUN = Tundra, SWP = warm or hot wetlands, swamp/marsh; locomotion groups: A = arboreal, AT = arboreal–terrestrial, T = terrestrial; mass categories: A = 0.5–8 kg, B = 8–45 kg; diet Level 1: F = frugivore, A = animalivore; diet Level 2: FG = frugivore–granivore, FH = frugivore–herbivore, FO = frugivore–omnivore, C = carnivore, I = insectivore.

Locomotion					**FW**			**IW**			**GS**	**TD**	**WL**
					RGD	**TBS**	**TRF**	**STW**	**SGW**	**TMC**	**MGS**	**TUN**	**SWP**
		A			4.0	8.4	12.1	1.4	4.3	6.1	0.5	0.0	4.0
			T		13.3	12.2	13.2	12.5	8.0	10.6	8.3	6.0	9.5
				AT	5.7	6.9	7.2	5.4	4.3	5.7	2.5	0.0	4.5
FW	**TBC**	1.7	6.7	4.0	-	*	*	-	-	-	-	-	-
	RGD	4.0	13.3	5.7		*	***	**	-	-	**	*	-
	TBS	8.4	12.2	6.9			-	***	*	-	***	**	-
	TRF	12.1	13.2	7.2				***	**	**	***	**	*
IW	**STW**	1.4	12.5	5.4					-	-	**	*	*
	SGW	4.3	8.0	4.3						-	-	-	-
	TMC	6.1	10.6	5.7							*	*	-
GS	**MGS**	0.5	8.3	2.5								-	-
TD	**TUN**	0.0	6.0	0.0									-

Body Mass			**FW**			**IW**			**GS**	**TD**	**WL**
			RGD	**TBS**	**TRF**	**STW**	**SGW**	**TMC**	**MGS**	**TUN**	**SWP**
	A		20.0	23.0	26.1	17.0	14.3	18.6	6.3	3.0	13.5
		B	5.3	6.6	9.7	5.3	4.0	5.9	2.5	1.5	6.5
TBC	12.0	1.7	-	*	**	-	-	-	-	-	-
RGD	20.0	5.3		-	**	-	-	-	*	*	-
TBS	23.0	6.6			***	*	*	*	***	**	-
TRF	26.1	9.7				***	**	**	***	**	*
STW	17.0	5.3					-	-	**	*	-
SGW	14.3	4.0						-	*	-	-
TMC	18.6	5.9							-	*	-
MGS	6.3	2.5								-	-
TUN	3.0	1.5									-

Diet 1				**RGD**	**TBS**	**TRF**	**STW**	**SGW**	**TMC**	**MGS**	**TUN**	**SWP**
		F		11.0	15.5	20.6	7.8	9.3	13.0	2.5	0.0	9.5
			A	14.3	13.9	15.0	14.4	8.3	11.9	5.3	4.5	10.5
FW	**TBC**	4.7	9.3	-	*	**	*	-	-	-	-	-
	RGD	11.0	14.3		*	***	-	-	-	*	*	-
	TBS	15.5	13.9			*	***	*	-	***	**	*
	TRF	20.6	15.0				***	**	**	***	**	*
IW	**STW**	7.8	14.4					-	-	**	*	-
	SGW	9.3	8.3						-	-	-	-
	TMC	13.0	11.9							*	*	-
GS	**MGS**	2.5	5.3								-	-
TD	**TUN**	0.0	4.5									-

Diet 2						**RGD**	**TBS**	**TRF**	**STW**	**SGW**	**TMC**	**MGS**	**TUN**	**SWP**
	FG					4.0	5.7	8.8	2.4	4.7	5.3	1.0	0.0	3.0
		C				10.3	10.0	9.4	8.1	6.0	8.3	3.5	3.0	5.5
			FO			4.0	6.2	6.7	3.1	3.7	3.9	0.8	0.0	3.5
				FH		3.0	3.6	5.2	2.3	1.0	3.9	0.8	0.0	3.0
					I	3.0	3.1	3.7	5.4	2.3	2.7	1.8	1.5	4.0
TBC	1.3	8.3	2.3	1.0	1.0	-	**	**	*	-	-	-	-	-
RGD	4.0	10.3	4.0	3.0	3.0		*	***	*	-	-	**	*	-
TBS	5.7	10.0	6.2	3.6	3.1			**	***	*	-	***	**	-
TRF	8.8	9.4	6.7	5.2	3.7				***	**	**	***	**	*
STW	2.4	8.1	3.1	2.3	5.4					*	**	**	*	-
SGW	4.7	6.0	3.7	1.0	2.3						-	-	-	-
TMC	5.3	8.3	3.9	3.9	2.7							**	*	-
MGS	1.0	3.5	0.8	0.8	1.8								-	-
TUN	0.0	3.0	0.0	0.0	1.5									-

Table 7.6.

Combined pairwise NPMANOVA and SIMPER results for Asian tropical mammal communities grouped by vegetation categories (Olson et al., 1983). Numeric values represent the average numbers of species in the analyzed vegetation categories. The asterisks represent statistically significant NPMANOVA results (*p<0.05; **p<0.01; ***p<0.001). Ecovariable categories in the top left of each individual table are those, which contributed to the differences between vegetation category pairs; the shading of the asterisks indicates which ecovariable is responsible for the highest contribution to the differences between two vegetation categories (SIMPER). Major ecosystem: FW=Forest and woodlands. Vegetation: RGD = tropical dry forest and woodland, TBS = tropical/subtropical broad-leaved humid forest, TRF = equatorial rain forest, STW = succulent and thorn woods and shrub, TMC = tropical montane complexes; locomotion groups: A = arboreal, AT = arboreal–terrestrial, S = subterranean, ST = subterranean–terrestrial, T = terrestrial, TA = terrestrial–aquatic; mass categories: A = 0.5–8 kg, B = 8–45 kg, E = 180–360 kg, F = 360+ kg; diet Level 1: F = frugivore, H = herbivore; diet Level 2: FG = frugivore–granivore, FH = frugivore–herbivore, FO = frugivore–omnivore, B = browser, G = grazer, C = carnivore.

Body Mass				**FW**		
				TBS	**TRF**	**TMC**
		A		16.9	25.2	17.5
			B	7.8	4.3	6.5
FW	**RGD**	23.0	10.0	-	-	-
	TBS	16.9	7.8		**	-
	TRF	25.2	4.3			*

Diet 2						**FW**		
						TBS	**TRF**	**TMC**
	C					9.9	10.3	10.5
		FG				4.8	7.2	4.0
			FH			5.1	7.1	5.5
				I		2.4	4.2	1.0
					B	6.3	5.9	5.5
RGD	14.0	5.0	7.0	3.0	6.5	-	-	-
TBS	9.9	4.8	5.1	2.4	6.3		*	-
TRF	10.3	7.2	7.1	4.2	5.9			-

FIGURE CAPTIONS

Fig. 7.1. 163 localities used in this study. For the list of names and coordinates, see Lintulaakso and Kovarovic, 2016: Appendix S1 in Supporting Information.

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