Chapter 16
Mammal Community Structure Analysis

Kris Kovarovic, Denise F. Su, and Kari Lintulaakso

Abstract Fundamentally rooted in Odum's niche concept, mammal community studies are based on the understanding that each resident species reveals information about its environment through its adaptations to specific resources and landscape features. Ecologists view the community's profile of strategies for exploiting particular spatial and dietary niches; a quantitative summary of these strategies when compared across locales from a variety of habitat types demonstrates striking similarities in the communities that live in similar habitats regardless of their location. Recognizing that communities can be compared across space, paleoecologists implemented community studies across time in an effort to reconstruct past environments. This synecological approach to paleoenvironmental reconstruction may be thought of as holistic, since it is not restricted to a single mammal family. However, thorough explorations of how fossil and extant communities differ have revealed significant dissimilarities brought about by the taphonomic history of paleontological assemblages. Techniques have been developed for addressing differences between the modern comparative community sample and the paleontological sample to which it is compared, but recent research conducted by both neo- and paleoecologists has suggested that there are unappreciated differences between modern habitats, as well.

Keywords Community analysis • Ecological diversity Ecomorphology • Niche • Taxon-free • Synecology

Introduction

Mammalian remains are often abundant at paleontological sites around the world and represent a critical source of information about the Earth's biological past. Individual species and entire assemblages can reveal the unique characteristics of the mammalian community in a given time and place, contributing to our understanding of how lifeforms evolved in different settings over geological time.

Many classic post-Darwin paleontological studies focused largely on morphological descriptions of mammalian remains for the sake of understanding species and, by extension, their reconstructed evolutionary relationships. Influential mid-20th century developments in modern ecological theory, however, spurred something of a revolution in mammalian paleo-sciences. A step-change in thinking arose with the extension of Odum's (1953) classic niche concept into the work of paleontologists who were interested in general interactions between the environment and mammalian evolution and reconstructing ancient environments. Paleontologists came to appreciate more fully that mammals could provide information about their habitats, and studies utilizing their remains in this manner added to a growing corpus of paleoecological literature.

There are numerous ways that mammals form an integral part of paleoecological research, from isotopic work (see Higgins 2018) to ecomorphology (see Barr 2018), but the focus here is on the analysis of entire communities, referred to variously as community structure analysis or ecological diversity analysis among other monikers. We review the

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theoretical underpinning for this synecological approach and its scientific development, consider its pros and cons compared to other available methods, and look ahead to further refinements that will allow us to elucidate ever more nuanced information about ancient environments.

Ecological Theory: The Underpinning of Community Structure Analysis

The Niche Concept

Eugene P. Odum is often credited with being one of, if not *the,* founder of the modern science of ecology. He was certainly not the only person in pre- or post-Darwin times to discuss connections between mammals and their environments (e.g., Hutchinson 1957, 1959) or to overtly outline the nature of relationships between the two (such as predator-prey interactions). However, Odum was a prime mover in an influential mid-20th century shift in ecological thinking. The general principles he championed are still persuasive and, despite some having been shown to be flawed in some respects, his work in the 1950s can be described almost as "contagious" in many scientific circles, particularly in debates surrounding the utility of evolutionary versus ecosystem ecology. One area where his intellectual input contributed greatly to the development of paleoecology is in the ecological niche concept, earlier defined by Elton (1927). Odum described this in the 2nd edition (1959) of his popular 1953 text *Fundamentals of Ecology* as "the position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior (inherited and/or learned)" (Odum 1959, p. 27). This he contrasted to a habitat, the physical space occupied by a species, employing an analogy that has endured for decades: the habitat is the species' "address", but the niche is its "profession".

The very language used here conveys something that is dynamic rather than static. It suggests that a niche is defined by relationships between individual species and between species and their physical environments and, furthermore, that these relationships can change over time. Indeed, by emphasizing that *structural adaptations* are a part of the very definition of a niche, an evolutionary time scale is invoked. Bodily structures are adaptations and, as such, they can tell us something about the niche(s) to which an organism was adapted (Harrison 1962). This isn't a circular concept so much as an empirical approach that enables us to work "backwards" – as paleontologists often do – by comparing what can be observed in the present with remains from the past; in this case, the hard tissue adaptive structures of the skeleton and dentition.

Although ecologically meaningful mammalian structural adaptations (also known as "ecomorphologies", a concatenation of the term "ecological functional morphologies") may be explicitly studied to infer past environmental conditions (see Barr 2018), community analysis uses information derived from these adaptations, as well as other proxies, to classify individual species into categories that broadly describe their preferred niches. The concept of a niche as expressed by Odum is also particularly pertinent here, as it makes clear that individual species have a place – their "position or status" – within a community, as well as within the ecosystem as a whole. The implicit idea is that the entire community can yield a greater amount of information about its environment than individual taxa, which occupy a limited range of niches, and therefore cannot provide a composite picture. Simply put, the whole is greater than the sum of its parts.

Mammalian Adaptations to the Niche

The exploitable niches that are available in a given habitat are conditioned by a combination of both biotic and abiotic factors, such as the different kinds of vegetation (trees, grass, herbs, shrubs, etc.) and the particular qualities of the soils in which they grow (drainage, nutrients, texture, inorganic composition, etc.) (Lomolino et al. 2006). These characteristics dictate what types of mammals can live in a given place and how they behave; a locale with nutrient-rich, moist but well-drained soil supporting heavy vegetation cover will have a very different mammalian community than a locale with dry, sandy soils and sparse vegetation cover. For example, tropical and subtropical rain forests or similar biomes with high annual average temperature and precipitation, where fruit resources are available year round, support more purely frugivorous mammals than areas with seasonal precipitation, which have higher numbers of herbivorous (folivorous) taxa (Kay and Madden 1997; Hanya et al. 2011; Pineda-Munoz et al. 2016).

A habitat can be divided into two distinct niches that are relevant for paleoecology: a spatial niche, which relates to the physical space in which a species moves during its life cycle, and the trophic niche, which relates to the diet on which a species relies to meet its nutritional and energy requirements. All mammals need a place to live and food to eat; thus, they are adapted to (or "fill") a particular spatial and trophic niche.

Soft-tissue structures are every bit as adaptive as hard tissue structures but are of limited use to paleontologists given their resistance to fossilization. However, the preservation of skeletal and dental remains, although impacted by numerous taphonomic factors, yields a wealth of material from the past that can be related back to spatial and trophic niche exploitation. Mammals negotiate and utilize space with different locomotor repertoires as evidenced by the morphology of their postcranial skeleton, particularly elements of the fore- and hind limb, which vary according to the substrate to which the species is adapted (e.g., Kappelman 1988).

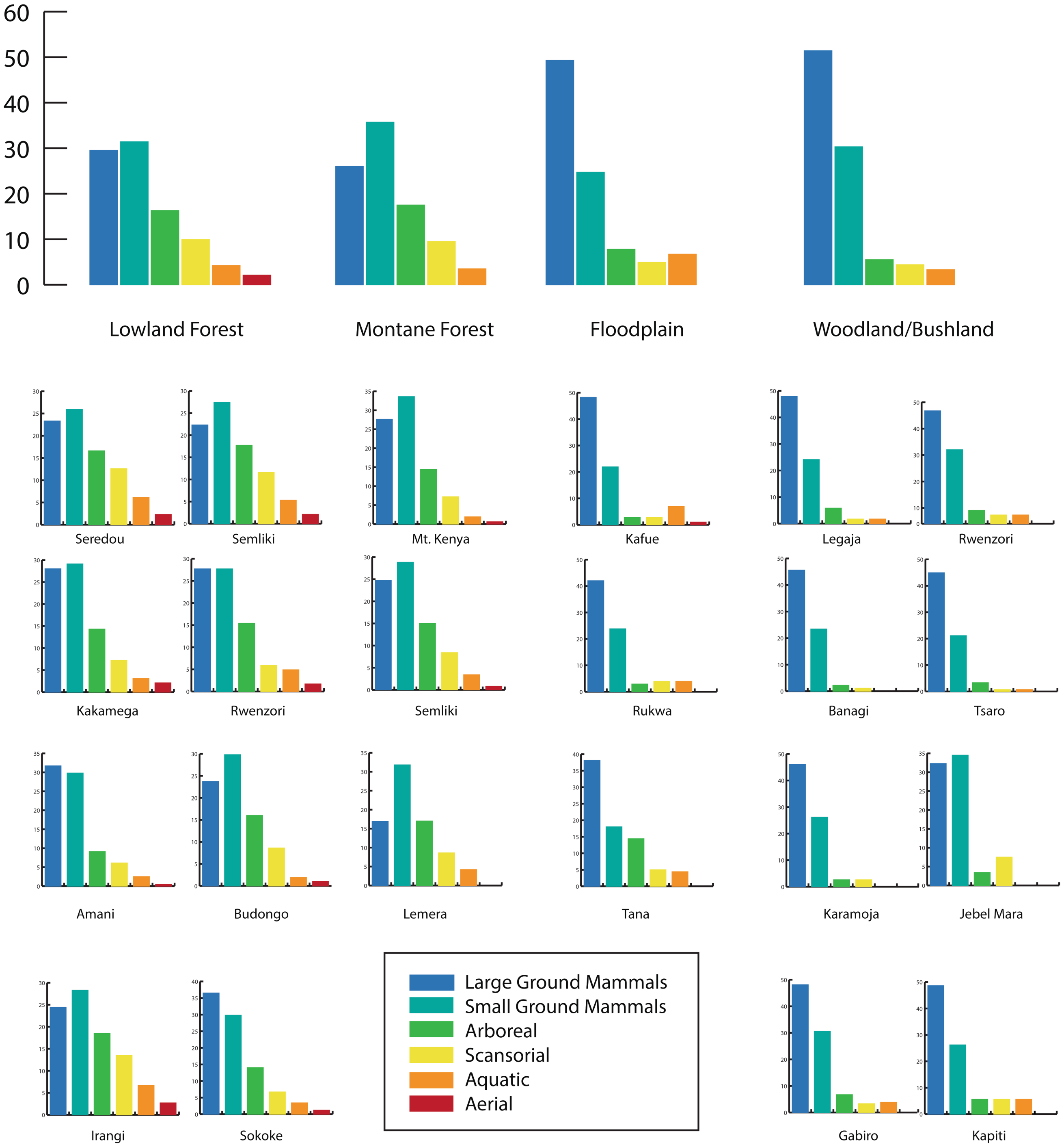

Fig. 16.1 Locomotor niche exploitation profiles from four habitat types in Africa, based on data from 22 modern mammalian communities. Data from Andrews et al. (1979)

Teeth, in comparison to postcranial elements, provide evidence regarding the trophic niche to which a species is adapted. Animals have specific dietary requirements and, thus, dental morphologies that are indicative of a carnivorous, insectivorous, frugivorous, or herbivorous diet. Combination niche exploitation strategies are particularly common in herbivores, which may be further defined as browsers (preferring dicots) or grazers (preferring grass) and, quite frequently, a mix of the two, which often relates to the seasonal availability of food sources. It is also common for herbivores on the browsing end of the spectrum to consume fruits and for insectivores to consume small mammals and/or fruit. True omnivores are rare, and the morphology of their dentition tends to point to a specific combination of dietary strategies rather than an equal reliance on all food resources (Pimm and Lawton 1978; Yodzis 1984; Pineda-Munoz and Alroy 2014).

Community Structure

The "structure" in a community structure analysis is essentially a summary of niche exploitation profiles. The primary interest is how the mammalian species fill trophic and spatial niches with their dietary and locomotor adaptations, although in many cases, body size is also considered as ecologically relevant and given the same consideration as the two primary niche profiles (Andrews et al. 1979). Summaries can be helpfully visualized in histograms, which demonstrate quite effectively a key concept of this analytical approach to environmental reconstruction: habitats with a similar array of available niches have similar community structure profiles, regardless of their geographical location. Figure 16.1, originally published by Andrews et al. (1979), expresses this in a series of histograms organized according to five broad habitat types. Profiles for the relative proportion of species in taxonomic orders, average body mass categories, and locomotor and trophic niche categories are presented. By comparing these profiles across the habitat categories, it is easy to see where differences between them occur in their mammalian faunas. For example, compare the lowland and montane forest locomotor profiles with those from non-forest habitats. Species in the large ground mammal category, which are entirely terrestrial, are found in much greater numbers in non-forests (approximately 50% of the fauna), whereas forests have a higher proportion of species classified as small ground mammals, which practice some form of arboreality in addition to exploiting the terrestrial niche. These data are from 22 modern localities in Africa, but the patterns can also be viewed on a broader geographic scale in datasets that extend to multiple regions and continents (Andrews 1996).

The phenomenon noted above is evident if one compares the profiles of the Central American tropical forest and Chinese paratropical forest in Fig. 16.2 (data from Andrews and Humphrey 1999). Although separated by some 14,000 km and millions of years of evolutionary history, these profiles are visibly similar, with approximately equal numbers of species in each category. The differences appear relatively minor; Chinese paratropical locales have a small number of aerial species that are lacking in the sampled Central American communities, which themselves have a slightly higher proportion of terrestrial taxa. But, overall, their general patterns are the same. This structural similarity in their faunal communities is indicative of the fact that all forests present a similar array of exploitable niches for resident species to fill.

Significance for Understanding Paleoecology

Paleoenvironmental community studies are fundamentally rooted in the present, based on observations of mammalian behavior in habitats where they are known to live. Demonstrating the existence of similarities in patterns of community structure in broad habitat categories was originally largely based on extant communities (e.g., Karr 1971; Fleming 1973), but an obvious next step for paleoecologists was to extend this principle to the fossil record. While direct observations of past mammalian dietary and locomotor habits cannot be made, their postcranial and dental remains provide evidence for their adaptive niches, from which community structure profiles can be constructed.

Andrews and colleagues (1979) developed the community structure technique for interpreting paleoecology based on early studies of species diversity in fossil and modern avian and mammalian communities (Kurtén 1952; Harrison 1962; Simpson 1964; Karr 1971). They noted that these early studies (Simpson 1964; Karr 1971) showed changes in the diversity of animal and plant species following a north-south gradient on different continents: as latitude decreased, the number of species increased. Additionally, the structure of the communities, i.e., distribution of body sizes and dietary and locomotor adaptations, also changed with latitude (Fleming 1973). They showed that community structure varies significantly with habitat type within a single latitudinal zone but that when both latitude and habitat type are similar, community structure is constant, regardless of differences in continent or species number and composition. They

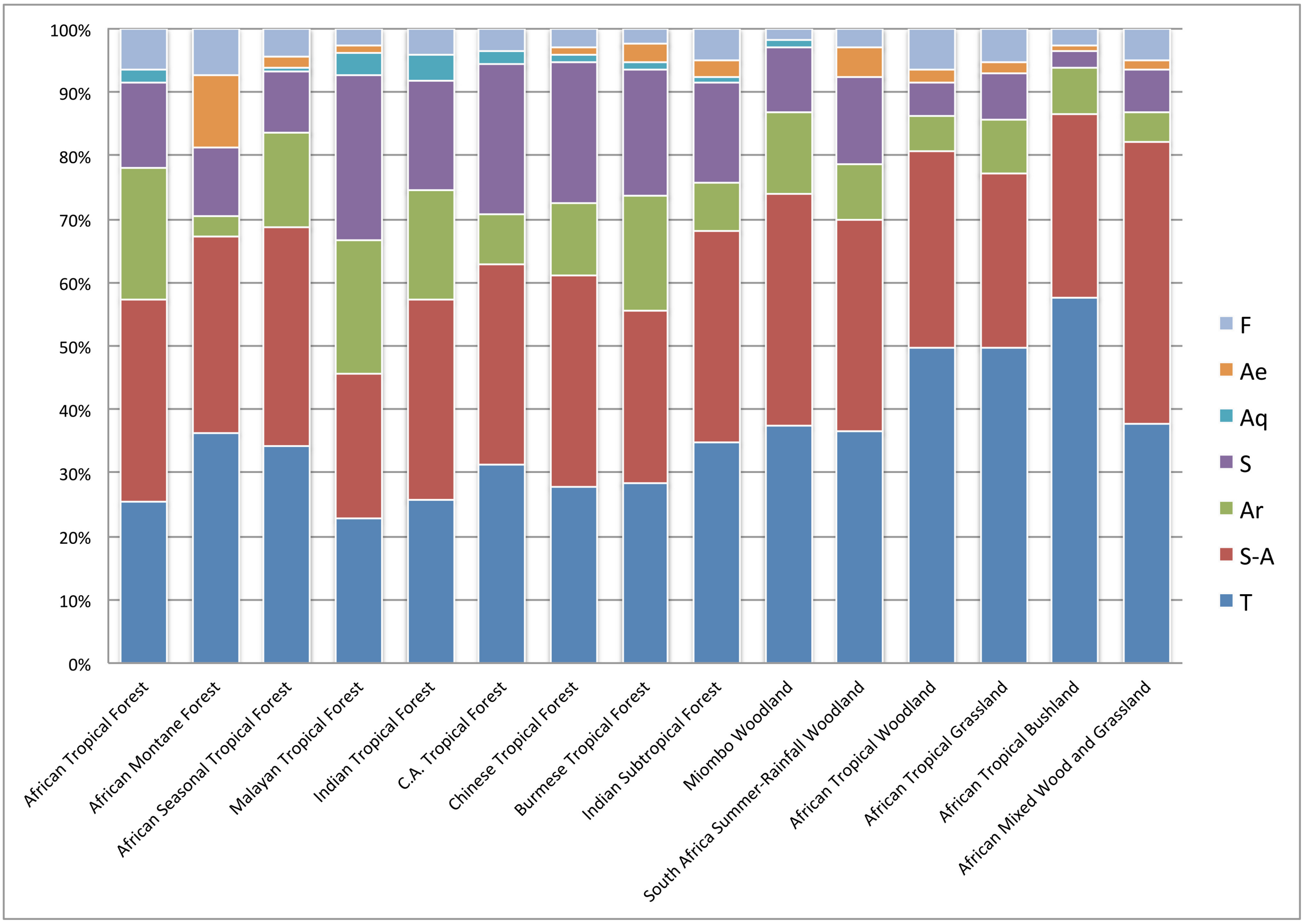

Fig. 16.2 Locomotor niche exploitation profiles for 15 habitat types from across the world, based on data from 44 modern mammalian communities. Data from Andrews and Humphrey (1999, p. 287). F = fossorial, Ae = aerial, Aq = aquatic, S = scansorial, Ar = arboreal, S-A = scansorial-arboreal, T = terrestrial

proposed that the habitat of a faunal community can be determined based on its community structure, irrespective of species composition, and that this predictive quality has direct application for paleoecology. By establishing patterns of community structure for a series of modern faunal communities and comparing them to those calculated for fossil communities, it is possible to make direct comparisons and inferences regarding the habitats from which the fossil assemblages may have come. This methodology was quickly integrated by many researchers into studies of the paleoecology of fossil hominoid-bearing faunal communities (e.g., Andrews and Van Couvering 1979; Van Covering 1980; Nesbit Evans et al. 1981) and is regularly incorporated into paleoecological studies of mammalian fossil sites today (e.g., Reed 1997; Kovarovic et al. 2002; Flynn et al. 2003; Su and Harrison 2007; Croft et al. 2008; Su et al. 2009; Meloro and Kovarovic 2013).

Paleoenvironmental Reconstruction

Bearing in mind the theoretical considerations of community structure analysis, there are also practical aspects to consider when implementing this method as a form of paleoenvironmental reconstruction. Decisions must be made regarding the selection of extant localities for the comparative dataset and how mammalian community niche exploitation profiles are compiled and categorized. The issue of categorization is particularly critical as neither mammalian niche exploitation behavior nor habitats are discrete entities, existing instead on a spectrum of related variables. Nevertheless, the method requires that species are classified according to their preferred niches and localities to their broad habitat or biome, which reduces the representation of their natural biological diversity. A balance must be struck between using a classification scheme that is nuanced enough to provide useful environmental interpretations and one that is also applicable to fossil species for which behavior is reconstructed from proxies rather than observed directly as in the modern world.

Extant Comparative Sample Selection

Assembling a dataset of extant localities against which to compare the target paleontological locality requires a careful and often lengthy process of identifying natural localities (i.e., ones not significantly altered by human habitation or activity) associated with complete mammalian species lists (Andrews et al. 1979). Many faunal lists for modern localities were compiled for specific research questions or conservation projects, and it is often the case that they record only the small or large fauna or species in particular families. Only localities for which faunal lists are considered complete are viable for community structure analyses, although establishing completeness itself may be difficult. Furthermore, the conflation of gamma (=regional) with alpha (=locality) species richness is also problematic, particularly when the faunal list has been assembled based on distribution maps, which may incorporate "expected occurrences" (i.e., a species is absent but marked as being present because the habitat is similar to where it is known to occur; for example, see Happold 1987). Needless to say, faunal lists based on alpha species richness are more appropriate for community structure analyses and should be used in favor of those based on the regional occurrence of taxa. Both of these factors can pose a challenge in selecting the appropriate comparative modern community. Fortunately, with the advent of electronic databases and data sharing requirements, there are a number of resources that can be useful in this regard; examples include species occurrence datasets, such as those published by the National Center for Ecological Analysis and Synthesis (NCEAS, https://www.nceas.ucsb.edu/), Ecological Archives (http://esapubs.org/archive/default.htm), DryadLab (http://datadryad.org/), and Biological Inventories of the World's Protected Areas (http://www.ice.ucdavis.edu/bioinventory/bioinventory.html), as well as specific peer-reviewed journals like Check List (http://biotaxa.org/cl/index) that focus on data related to species geographic distributions. A good starting point for finding information to assist with standardizing these occurrence data (which quite often are from national parks and similar areas) is the World Database on Protected Areas (WDPA, https://www.protectedplanet.net/).

In addition to being suitable from a sampling standpoint, localities should generally encompass the entire spectrum of ecological possibilities. However, it may be possible to exclude certain major biomes depending on the specific research question or location of the paleontological site being subjected to environmental reconstruction. There may be reasonable grounds for excluding temperate and Arctic tundra communities, for example, if the paleocommunity is derived from an equatorial location where other indicators suggest that it was not physiognomically similar to tundra (e.g., desert in the tropical realm).

Gross vegetation physiognomy is, in fact, one of the best defining characteristics for any habitat classification system. There are many systems available in the literature, some of which span the entire range of global biomes, but they are often based on specific vegetation species associations (White 1983; Eiten 1992; Lawesson 1994). But, just as a community structure analysis does not account for the taxonomic identity of the mammalian species, it also cannot account for the species of vegetation in the habitats. Structural variables such as the number of canopies, crown height, overall tree, bush, or shrub cover and the presence of grassy or herbaceous ground cover are more relevant. Of course, such systems can be rather coarse, lumping several habitat types into broad groups that obscure ecological nuances that exist between them. The system used by Andrews et al. (1979) in Fig. 16.1 considers only four categories, including one for all woodlands and bushlands; although it is rather reductive, it also presents a series of rules that make it reasonably easy to place each locality into a habitat group. The more nuanced the habitat classification system, the more information that can be extracted from a paleocommunity, but the harder it becomes to categorize the habitat groups in the first place. Since they exist on a continuous spectrum of vegetation cover, the difficulty is in knowing where to draw the line to create discrete, analyzable categories. For this reason, paleoecologists have drawn on current research and descriptions of extant vegetation communities and habitats (particularly White 1983 and Olson et al. 1983, 1985) to devise clearly-defined classification systems that can be applied to the paleontological record (Andrews et al. 1979; Reed 1997; Andrews and Humphrey 1999). Table 16.1 (originally from Kovarovic et al. 2002) summarizes the habitat categories of 22 modern localities used in a community structure analysis of the Upper Ndolanya Beds of Laetoli, a Pliocene hominin-bearing site. The habitat type column represents the broad classification system employed, while a more detailed description of each locality provides the basis for the categorization and aids in subsequent interpretations.

It is important to note that vegetation structure and diversity are strongly correlated with annual rainfall (Gentry 1988); consequently, species richness and community

Table 16.1 Twenty-two modern African localities classified by habitat. Modified from Kovarovic et al. (2002), which is based on the habitat classification system first outlined by Andrews et al. (1979)

Locality	Country	Habitat type	Description
Irangi	Zaire	Tropical forest	Lowland evergreen forest; primary and secondary-riverine cultivation types
Seredou	Guinea	Tropical forest	Lowland evergreen forest
Semliki a	Uganda	Tropical forest	Lowland semi-deciduous forest
Budongo	Uganda	Tropical forest	Lowland semi-deciduous forest; secondary and monotypic types
Semliki b	Uganda	Montane forest	Montane evergreen forest continuous with lowland
Mt. Kenya	Kenya	Montane forest	Montane evergreen forest; primary and secondary
Lemera	Zaire	Montane forest	Montane evergreen forest in river valley
Amani	Tanzania	Seasonal tropical forest	Intermediate semi-deciduous forest
Kakamega	Kenya	Seasonal tropical forest	Intermediate semi-deciduous forest, secondary with glades, hills with bush
Rwenzori Forest	Uganda	Seasonal tropical forest	Lowland semi-deciduous forest
Sokoke-Gedi	Kenya	Seasonal tropical forest	Lowland deciduous forest and woodland
Tana River	Kenya	Mixed wood and grassland	Floodplain grassland with patches of deciduous forest
Gabiro	Rwanda	Mixed wood and grassland	Wooded grassland next to lake flats
Legaja	Tanzania	Mixed wood and grassland	Lake in short grassland with woodland on the fringes
Rukwa	Tanzania	Mixed wood and grassland	Floodplain grassland with bordering woodland and swamps
Rwenzori	Uganda	Tropical woodland	Short grass plains-bush-woodland mosaic
Banagi	Tanzania	Tropical woodland	Deciduous woodland and bushland
Kafue	Zambia	Tropical grassland	Floodplain grassland with bordering woodland
Serengeti	Tanzania	Tropical grassland	Short grass plains with small patches of bush
Karamoja	Uganda	Tropical arid bushland	Arid bushland
Kapiti Plains	Kenya	Tropical arid bushland	Grassland-bushland mosaic
Tsavo	Kenya	Tropical arid bushland	Bushland and arid bush

structure will also vary in relation to annual rainfall (Kay and Madden 1997). It has been shown that in tropical South American faunal communities, there is significant positive correlation between rainfall and species richness and abundances of frugivores, arboreal mammals, and herbivorous mammals, among other attributes (Kay and Madden 1997). In fact, it is possible to use these relationships to predict annual rainfall in past environments (Kay and Madden 1997). Thus, it is important to take into account the diversity of annual rainfall sampled by the comparative modern communities when reconstructing the paleoenvironments of past communities.

Fossil Assemblage Suitability

Not all paleontological localities can be subjected to a community structure analysis. The assemblage must preserve a reasonably high proportion of the mammalian fauna that existed. Although most sites will suffer some amount of taphonomic loss depending on a variety of ecological and depositional conditions, an assemblage that is noticeably lacking in overall species number, or richness, is not a good candidate for this methodology (Andrews 1996). It is difficult to judge the completeness of a community in the fossil record, but some basic protocols can be applied to determine whether an assemblage is suitable.

One point to consider is the number of taxa that are required purely from the standpoint of multivariate statistical robusticity. From this perspective, even an assemblage with a low number of species, as few as five or six (Louys 2007; Louys et al. 2009), can be used. However, communities with such low species richness are obviously depauperate when compared to the richness observed in natural modern communities. Theoretically speaking, habitats that are structurally and topographically complex, such as forests and complex woodlands, provide a greater number of niches to exploit and therefore have greater richness (Reed 2008). In the tropical realm, it is uncommon to find communities with fewer than 40 taxa across all body sizes; this value is approached only by communities inhabiting quite open environments (e.g., Serengeti Plains; Andrews and Nesbit Evans 1979; Andrews et al. 1979). While this might be a useful threshold to consider given that the number is reflected by extant faunas, it is an unreasonable expectation of many fossil communities, which tend to average lower than 40 taxa (see, for example, Andrews and Nesbit Evans 1979) for reasons pertaining to taphonomy (Badgley et al. 1995), the intensity of scientific sampling (it is known that bigger samples tend to have more species; Croft 2013; Su 2016) and our ability to correctly identify all individual fossil species from fragmentary remains. Furthermore, the proportion of each taxon in the sample and the distributional pattern of the taxa that make up the faunal community are all factors that affect the accuracy of predicting the correct habitat association for the fauna (Mares and Willig 1994). Even when these factors are known, as in modern communities, a large proportion of the fauna is often required to be confident of the habitat association of the community (Mares and Willig 1994). In an extensive exploration of the species richness required to effectively distinguish between modern habitats, Louys et al. (2009) found that this varied depending on broad habitat type as defined by vegetation structure (closed, mixed, or open). They provide empirical support for what makes intuitive sense; richness is generally correlated with broad habitat type, so it is expected that a greater number of species might be required to distinguish between those that are taxonomically richer. A minimum of 32 species was identified as the threshold for distinguishing between communities adapted for closed and mixed habitats, whereas only 12 were required to distinguish between open and mixed, and eight for open and closed (Louys et al. 2009).

Ecovariable Categories

Community structure analysis considers three variables that reflect the niche exploitation of the species, also termed ecovariables: body size, locomotor adaptation, and feeding preference. Their expression provides information on how the species of a mammalian community fills the spatial and trophic niches of the ecosystem.

Body size (mass): Body size is one of the most fundamental biological characteristics of mammals. It has been shown to correlate significantly with other aspects of biology and behavior and is an important factor in space utilization for an organism. Various studies have shown a correlation between body size distributions of mammalian communities and their environments (e.g., Legendre 1986, 1989; Gingerich 1989; Croft 2001; Flynn et al. 2003; but also see Rodríguez 1999 for a dissenting opinion), although it appears to be the least discriminating of the three ecovariables (Andrews 1996; Reed 1997; Lintulaakso and Kovarovic 2016). Body size classification in extant mammals is relatively straightforward, done by calculating the mean of the species' weight range. Reconstructing body size in fossil mammals is more complicated, and is based on the consistent isometric and allometric relationships between various skeletal dimensions and body mass (e.g., Gould 1975; Alexander 1977; Fortelius 1990; Gingerich et al. 1982; Scott 1990; Legendre 1986; references in Damuth and MacFadden 1990; see Hopkins 2018 for detailed discussion and additional references). For the most part, because community structure analysis relies on the mammalian species list, and species identification is dependent on craniodental material, the methodology uses dental dimensions as body size proxies. It is an added advantage that teeth are the most identifiable and preserved element in the mammalian fossil record and that various dimensions are known to correlate with body size, among them molar surface area and tooth row length (Gould 1975; Gingerich et al. 1982; Fortelius 1990; Hopkins 2008, 2018). It is worth noting that although there are many factors that can influence the robustness of body size estimation (see Hopkins 2018 for detailed discussion), precision is not as crucial in community structure analysis because species are categorized in ranges of body masses that compensate for any inexactness in the predication. Body size categories vary from study to study and can have as few as three categories (<1 kg, 1–45 kg, >45 kg; Andrews et al. 1979) to as many as 12 categories (see Table 2 in Townsend et al. 2010). The division of body size categories is arbitrary to a certain extent, but it is important to consider the body size distribution of the target paleocommunity so that body size categories are not overly or under-divided.

Locomotor adaptation (substrate categories): Locomotor adaptations are generally considered in terms of the substrate or spatial niche for which the organisms are adapted (Harrison 1962; Eisenberg 1981). Assignment of a locomotor class should be based on the morphological adaptations of the limb bones that allow the species to move within its niche (see Dunn 2018). However, there are instances, particularly within a fossil assemblage, where it is often not possible to associate isolated postcranial elements to taxonomically identified craniodental materials; in such cases, it may be necessary to categorize a species based on specimens of from other sites or, as a last resort, from taxonomic analogy.

Locomotor categories are relatively broad and emphasize ecological niche structure; the animals in a community are categorized to correspond to the physical layers in the environment (Andrews et al. 1979). The categories proposed by Andrews et al. (1979) and commonly used in community structure analyses are: (1) aerial, the space above the vegetation to which aerial mammals, such as bats, are restricted; (2) arboreal, mammals that are found solely in the upper canopy or small branch zone of trees; (3) scansorial, mammals that are found in the middle and lower canopy and often climb up and down trees; (4) terrestrial-scansorial, terrestrial mammals that are not restricted to the ground and often utilize the lower branches of trees; (5) terrestrial, mammals that are restricted to the ground; (6) fossorial, mammals that burrow in the ground; (7) aquatic, mammals that inhabit bodies of water. Combination niche categories are also possible, e.g., terrestrial-arboreal or terrestrial-aquatic, as some species equally exploit the tree canopy and the ground, or underground dens and the land surface, albeit often for different sorts of activities like eating, sleeping and rearing young. There are also specialist niche exploitation categories, such as cursorial, which indicates a species that is well-adapted for running long distances over relatively open ground (see also Barr 2018), although they are generally considered part of the terrestrial category. Later studies have further combined the arboreal and scansorial categories and re-named terrestrial-scansorial to terrestrial-arboreal and included all mammals that use both substrates (e.g., Reed 1997; Su and Harrison 2007), while others have further refined the categories to accommodate the suite of specializations that allow the animal to exploit more than one ecological zone (e.g., Kovarovic et al. 2002). The less refined the categories, the easier it will be to assign fossil taxa to the appropriate category; however, it may also result in a decreased ability to distinguish between faunal communities. Most studies exclude the aerial category in their analysis due to the paucity of bats in the fossil record and the rarity of gliding mammals in both modern and fossil communities (Andrews et al. 1979; Reed 1997; Kovarovic et al. 2002; Su and Harrison 2007; among others).

Dietary adaptations (trophic categories): Trophic categories are assigned on the basis of the primary dietary adaptation of the animal, usually inferred from tooth morphology (specialization of molar cusps, degree of hypsodonty, canine morphology or reduction; see Evans and Pineda-Munoz 2018), wear patterns (mesowear and microwear; see Green and Croft 2018), and/or stable carbon isotope composition (see Higgins 2018). The use of multiple proxies to infer the diet of fossil mammals can sometimes result in contradictory reconstructions where the lines of evidence do not align; for example, stable carbon isotope data may suggest that the species consumed both browse and graze even though its teeth are hypsodont (e.g., alcelaphin species from Laetoli; see Kingston and Harrison 2007). This can reflect the difference between fundamental niche and realized niche (Hutchinson 1957) and, where these data are obtainable, categorization should be based on what a species is actually eating at that particular site rather than its morphological adaptation. Furthermore, in some cases, so little of a species is preserved or its ecological behavior is so little understood that one must default to the behavior of its relatives (extinct or extant) or "average" what is known about its genus or family.

The trophic or dietary categories to be used could include: (1) carnivore, animals that consume meat as a majority of their diet irrespective of taxonomic classification; can be further subdivided into animals that consume only meat, animals that consume meat and bone, and animals that consume meat and invertebrates; (2) insectivores, animals that eat mostly insects irrespective of taxonomic classification; (3) grazers, animals that mostly eat grass or specific types of grass from edaphic grasslands (i.e., where drainage is impeded and there is often seasonal flooding); (4) browsers, animals that mostly eat products of dicot bushes and trees; (5) mixed feeders, animals that eat both dicot and monocot leaves; (6) frugivores, animals that eat mostly fruits; can be further refined to animals that eat fruits and leaves and animals that eat fruits and insects (but often combined because it is difficult to distinguish these two categories based on ecomorphology); (7) omnivores, animals whose diet is wide-ranging and consists of food from more than two trophic categories; (8) root and tuber eaters, animals that specialize in roots and tubers. The use of categories varies across studies; the difference is primarily in the degree of refinement in category definitions and the use of combination categories (e.g., carnivore vs. carnivore-meat, carnivore-bone, carnivore-invertebrate; see Reed 1997 vs. Kovarovic et al. 2002). Additionally, at sites that predate the middle to late Miocene spread of true C_4 grasslands, herbivorous animals are more correctly categorized as folivorous "open habitat feeders" and "closed habitat feeders" (see Dunn et al. 2015). As is the case with choosing locomotor and substrate categories, it is easier to assign a fossil taxon to a broader category, particularly if the ecology of the fossil species is not well known; however, this may also result in greater overlap in the community structure of faunal communities and make it more difficult to distinguish among them.

Multivariate Statistics for a Multivariate Problem

Since its inception, analyses of community structure have included univariate, bivariate, and multivariate comparisons. Profiles of community structure in histograms (e.g., Andrews et al. 1979a; Nesbit Evans et al. 1981; Kovarovic et al. 2002) and bivariate plots of ecovariables (e.g., Reed 1997, 2008; Kovarovic et al. 2002) are useful interpretative tools and can demonstrate ecological relationships; for example, the proportion of frugivorous mammals is inversely related to that of grazing mammals, with forest habitats having more frugivorous species and open habitats having more grazing species (see Fig. 16.3). Univariate statistical tests are also appropriate when testing the null hypothesis that mean proportions of ecovariables are the same between habitat categories. For example, Reed (2008) used a single factor ANOVA to test the null hypothesis followed by the "Tukey honestly significant difference for uneven sample sizes" post-hoc test for differences between pairs of habitats for each ecovariable.

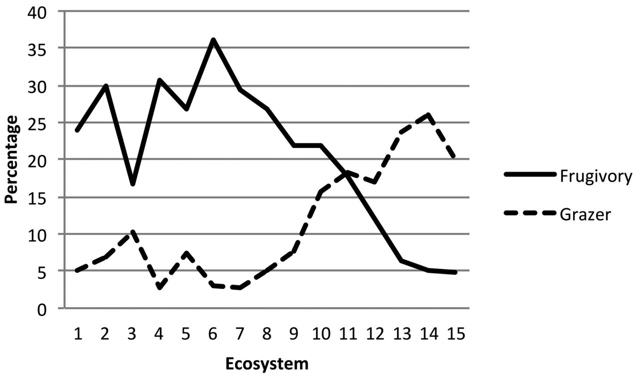

Fig. 16.3 Percentage of frugivorous and grazing species in modern ecosystems. More open habitats (ecosystems 10–15) have higher proportions of grazing species and lower proportions of frugivorous species. More wooded habitats (ecosystems 1–9) have the opposite pattern, with higher proportions of frugivorous species and lower proportions of grazing species. Ecosystems: 1 = African tropical forest, 2 = African montane forest, 3 = African seasonal tropical forest, 4 = Malayan tropical forest, 5 = Indian tropical forest, 6 = Central American tropical forest, 7 = Chinese paratropical forest, 8 = Burmese subtropical forest, 9 = Indian subtropical forest, 10 = Miombo Woodland, 11 = South African summer-rainfall woodland, 12 = African mixed wood and grassland, 13 = African tropical woodland, 14 = African tropical grassland, 15 = African tropical arid bushland

Although other approaches can be used, community structure is fundamentally a multivariate problem and requires robust multivariate statistical techniques. It is important to note that multivariate analysis does not actually provide environmental data; rather, it organizes the data by ordination or classification in such way as to allow for visualization of the data and environmental interpretations (Andrews 1996). Different multivariate analyses have been used in studies of community structure and are summarized as follows.

(1) **Hierarchical clustering analysis**: A type of cluster analysis in which a hierarchy is built using a measure of distance between pairs of observations, typically shown as a dendrogram (for examples of application, see Andrews 1996; Kovarovic et al. 2002; Su 2011).

(2) **Principal components analysis (PCA)**: An ordination technique in which the data are transformed into uncorrelated variables called principal components. The first principal component contains as much of the variability of the data as possible, and each remaining component contains as much of the remaining variability as possible (Zuur et al. 2007). The results are usually presented as a bivariate plot of its first and second principal components, which should contain most of the variance of the data (for examples of application, see Kovarovic et al. 2002; Flynn et al. 2003; Su and Harrison 2007).

(3) **Principal coordinates analysis**: An ordination technique similar to PCA that uses a distance matrix instead of data transformation (Zuur et al. 2007); it is sometimes preferred to PCA because correlations within the ecological data matrix are generally weak (Andrews 1996; this reference also provides an example of its application). Principal coordinates analysis can be followed by a canonical analysis (called a discriminant analysis when the interest is in group membership and a correlation analysis when the interest is in relationships with environmental variables) that allows for constrained ordination on the basis of any distance or dissimilarity measure (Anderson and Willis 2003; see Fig. 16.4 for an example of its application).

(4) **Non-metric multidimensional scaling**: A non-metric ordination method designed to circumvent the assumption of linearity in principal coordinates analysis. Instead, it uses rank order information in a dissimilarity matrix to carry out iterative multidimensional scaling that produces differences in distribution and clustering that is analogous to the components in principal components analysis (Andrews 1996; this reference also provides an example of its application).

(5) **Correspondence analysis**: A geometric technique used to visualize the associations between the levels of a two-way contingency table; rows and columns of the table are displayed as points in a low-dimensional space that is consistent with their associations in the table (Greenacre 1984). For examples, see Greenacre and Vrba (1984), Reed (2008), Kovarovic et al. (2013), and Su and Haile-Selassie (in press).

(6) **Discriminant function analysis**: A statistical technique used to predict a categorical dependent variable (i.e., group membership) by one or more continuous or binary independent predictor variables. See Croft et al. (2008) and Su and Haile-Selassie (in press) for examples of the application of this technique and Kovarovic et al. (2011) for a review of some important considerations of this method.

The choice of which multivariate analysis to use depends on the questions being asked by the researcher as well as the data themselves, as analyses often have different assumptions (see citations above for computational details). Different analyses are not mutually exclusive and are often used in conjunction with one another. With analyses that deal with proportional data, as is the case with community structure data, transformation of the raw data is often necessary. Sokal and Rohlf (1995) proposed using the arcsine square root transformation for these types of data, and this has been widely adopted since then by ecologists and paleoecologists alike (Warton and Hui 2011). There are other types of transformation that can be used (e.g., logit transformation; Warton and Hui 2011); the choice of transformation and, importantly, its necessity, is determined by the research question and the assumptions made about the data (Clarke and Warwick 1994; Kindt and Coe 2005).

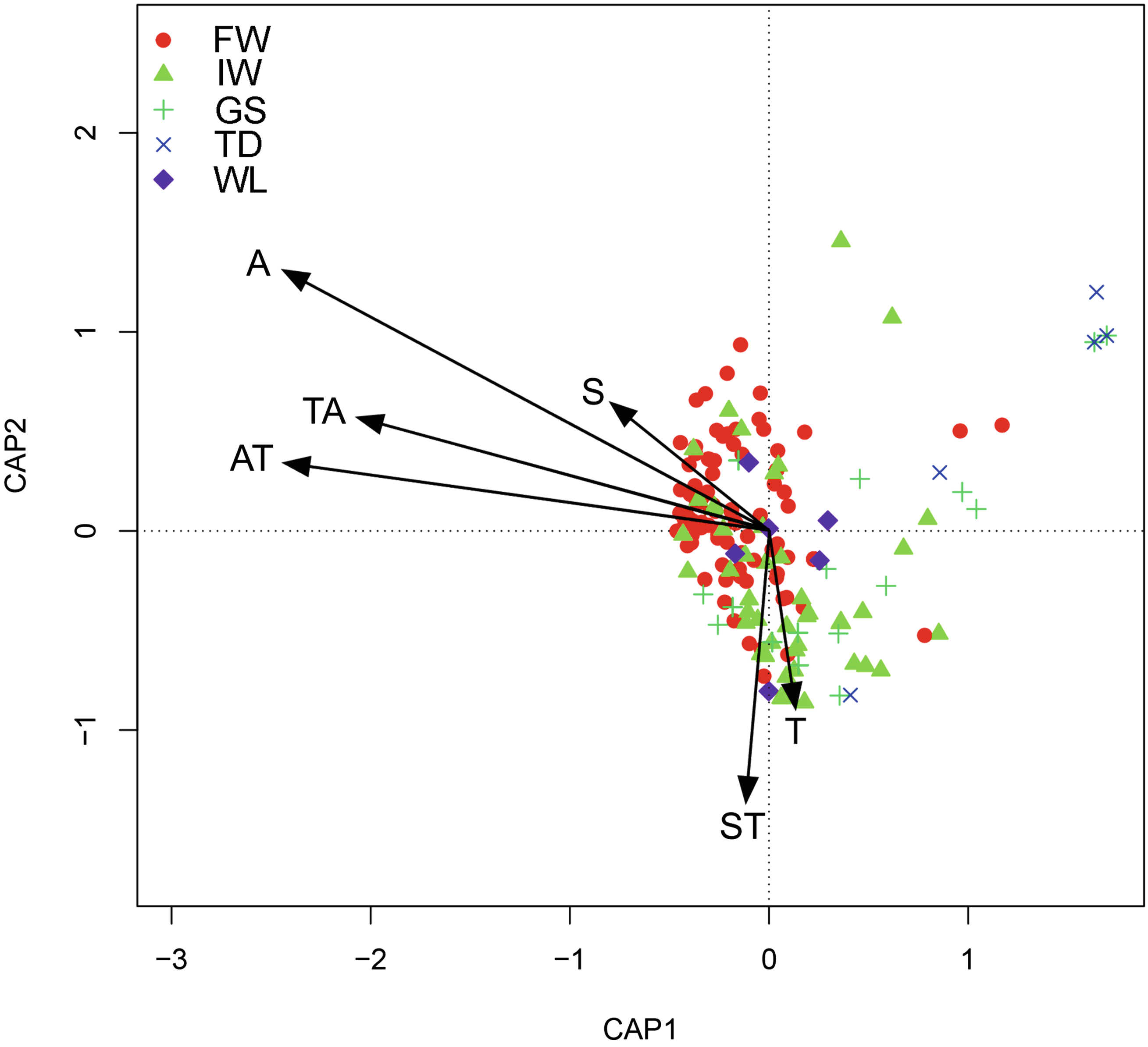

Fig. 16.4 Canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) for 169 tropical mammal communities (see Lintulaakso and Kovarovic 2016). The communities are analyzed by the number of mammalian species within locomotion groups. Communities are grouped by Olson et al. (1983) major ecosystems. Two main principal coordinates are displayed. CAP1 is associated with a low number of arboreal species. Therefore, forested, more closed environments (FW) can be identified by a high negative correlation of low numbers of arboreal (A) or arboreal–terrestrial (AT, TA) species. CAP2 is associated with a low number of subterranean–terrestrial (ST) or terrestrial (T) species. Here, the more open environments (IW, GS) can be identified by a high negative correlation of low numbers of subterranean–terrestrial or terrestrial species. Tundra and desert (TD) has a relatively high positive correlation with both CAP1 and CAP2, having a low number of any species within the locomotion groups. Wetland (WL) communities are scattered all over the plot, having no real association with any of the CAP axes. This plot also shows some outliers that could be investigated further as a potential source of error. For example, the outliers may pertain to a locality that was misclassified a priori into an ecosystem group, the species list for the locality may not be complete, or the species list may have been collected from a number of ecosystems within a single locality. Major ecosystems (Olson et al. 1983) are: major forest and woodland (FW), interrupted woods (IW), grass and shrub complexes (GS), tundra and desert (TD), and major wetlands (WL)

Strengths of Community Analysis

The utility of the community structure approach for reconstructing past environments is multi-faceted: it makes use of what is often ample and easily accessible data (fossil remains); it is grounded in a solid theoretical context, the main principles of which (i.e., adaptation, niche exploitation) can be clearly observed in the modern natural world, so comparative data are plentiful and reliable; and it is based on a complete mammalian community as defined by the ecological relationships that exist between species and their environments. Some challenges do exist to utilizing the approach, and these are detailed later in this chapter, but here we outline some of the more nuanced advantages to selecting this method over others, illustrated with examples.

An All-Inclusive Approach

Community structure analysis is holistic in that it can include both micro- and macromammals. This is desirable because they relate to different aspects of their environment, including scale, and therefore provide complementary information on niche exploitation. Smaller taxa tend to more regularly exploit fruits and seeds and are able to more efficiently exploit the arboreal and underground substrates in comparison to larger, generally more terrestrial species. Small species are also prey animals for larger carnivores reliant on meat consumption, while smaller species with carnivorous diets tend to eat a combination of small animal protein and insects, or insects in combination with other resources. These differences suggest that eliminating smaller body mass categories from an analysis would also eliminate important ecological information provided by the many frugivorous, insectivorous, fossorial, and arboreal taxa present. These niches, in essence, would be under-represented, and discrimination of habitat types would be based on a limited array of niches, thus blurring the boundaries between them.

However, many paleontological sites present a taphonomic bias against the preservation of smaller-bodied species that can make their inclusion analytically challenging (e.g., Kovarovic et al. 2002; see “Analytical Challenges” below). Additionally, some taxonomic units are traditionally left out of this type of analysis for other practical and ecological reasons. Volant mammals (i.e., Chiroptera) are excluded because of their rarity in the fossil record (Andrews et al. 1979; Reed 1998; Kovarovic et al. 2002; Mendoza et al. 2004; Louys et al. 2011). Although this group displays diverse ecological niche adaptations (bats vary considerably in body mass and diet across a wide spectrum) and therefore should be useful for discriminating among modern habitats, they are of limited utility in the fossil record. Mammals restricted entirely to aquatic environments, such as Cetacea (whales and dolphins) and Sirenia (manatees and dugongs), are also often left out of such analyses because it is the terrestrial habitat that is generally of interest at paleontological sites (although marine mammal community analyses can be conducted in their own right; e.g., Schick et al. 2011). Including an aquatic or semi-aquatic category is often done to allow for categorization of mammals that are partly adapted for an aquatic lifestyle but that still exploit the terrestrial environment in some fashion, such as hippopotami, otters, beavers, and similar species. This allows some element of water availability to be considered implicitly without direct reference to the geological evidence.

“Taxon-Free”: Ecology Versus Species Diversity

When taken as a sum of available niches and the proportion of species that exploit them, as in the case of a community structure analysis, a paleohabitat can be viewed without specific reference to the identity of the resident species; in a sense, this method may be thought of as “taxon-free”. This is perhaps one of the most important aspects of the method, since paleospecies can be difficult to classify taxonomically (see discussion in “Analytical Challenges” below). Taxonomic considerations in a paleocommunity analysis are thus restricted to the determination of how many species are present (which, admittedly, is not always an easy task) rather than their exact identities or phylogenetic relationships, a somewhat separate area of study often under revision. What matters for a community structure analysis is what the individual species were doing as evidenced by their adaptations to particular niches. Diversity of ecological relationships and niche exploitation strategies employed by a community are far more relevant than number of species alone.

Being unencumbered by taxonomy removes the reliance on “indicator species” in paleoecological reconstructions. This approach, which is implicitly imbued with the principle of taxonomic uniformitarianism, was a favored analytical tool in earlier paleoecological work (e.g., Coe 1980; Vrba 1980; Greenacre and Vrba 1984). Much rigorous research went into determining which species are ecologically consistent in the modern world based on the idea that they were likely to have behaved similarly in the past; one frequently cited example of this approach is the Antilopine-Alcelaphine Criterion (AAC) developed by Vrba and colleagues (Vrba 1980; Greenacre and Vrba 1984), which was applied to many sites in the East and South African paleoanthropological record (Kappelman 1984; Potts 1988; Shipman and Harris 1988). The AAC method was based on observations of extant bovid tribes and their tendency towards the consistent exploitation of specific trophic and spatial niches. Some tribes, such as the antilopines and alcelaphines, are known to prefer the resources of open, arid habitats where they comprise 60% or more of the bovid fauna. When compared to the proportion of species in other tribal pairs such as Bovini and Reduncini, representing wetter, closed habitats, and Tragelaphini plus Aepycerotini (the impala, *Aepyceros melampus*), indicating dry and closed habitats, this criterion was understood to be a powerful predictor of paleoenvironment, particularly gross vegetation physiognomy. However, despite strong evidence that ecological similarities in closely-related bovid taxa may be the result of evolutionary constraint and canalization of traits, not all tribes have had such stable ecological strategies over the same time scales (Sponheimer and Lee-Thorp 2003; Faith et al. 2014; Behrensmeyer 2015; Cerling et al. 2015) or are known to include species that are evolutionarily sensitive to ecological change, such as the alcelaphine hartebeest, *Alcelaphus buselaphus* (e.g., Flagstad et al. 2001) or the impala and its extinct relatives in the genus *Aepyceros* (Faith et al. 2014). For reasons such as these, indicator species are approached with some caution. The AAC method has not been abandoned, but it is used more conservatively and almost always in conjunction with other proxies, such as non-mammalian indictors, stable isotopes, and/or depositional conditions (e.g., Schrenk et al. 1995; Sponheimer and Lee-Thorp 2003; Campisano and Feibel 2007; Bedaso et al. 2013). Community structure analyses are also often discussed in light of the taxonomic composition of the target community with particular reference to specific indicator taxa, but this is used to inform or support the main interpretations derived from the community analysis itself (e.g., Su 2016).

Time and Space

Mammalian communities, being sensitive to ecological conditions, are especially useful when reconstructing habitats across a broad stretch of time or space (e.g., Fortelius et al. 2002). This is borne out by research in extant communities, particularly in small mammal communities, which experience turnover and re-assembly rapidly enough that they can be observed over historical time periods or after a known environmental event that shifted habitat distributions, as well as on spatial scales where observations of presence/absence and ecological behavior are easily made (e.g., Williams et al. 2002; Thibault et al. 2004; Thibault and Brown 2008). Macromammal evidence is less well established but also suggests that communities change quickly in response to shifts in climate and that these changes are recorded in assemblages of skeletal and dental remains on modern landscapes (e.g., Western and Behrensmeyer 2009).

In paleontological locations where the fauna is known to have changed taxonomically over time, a full community analysis can bring greater insight to the ecological conditions that supported these different communities. Good examples of this approach are from the paleoanthropological sites of Laetoli and Olduvai in the southern Rift Valley in northern Tanzania, where a significant amount of paleoecological work has been conducted in an effort to understand the environmental context of three hominin genera throughout the Pliocene and Pleistocene: *Australopithecus, Paranthropus*, and *Homo.*

At Laetoli, *Australopithecus afarensis* is found in the 3.8–3.6 Ma Upper Laetoli Beds and *Paranthropus aethiopicus* in the 2.66 Ma Upper Ndolanya Beds (Leakey and Harris 1987; Harrison 2011). Community structure analyses indicated that the older beds were more wooded (Andrews 1989; Reed 1997) than early interpretations based on indicator species or single-family studies that emphasized the presence of terrestrial and grazing taxa (Leakey and Harris 1987). The composite mammalian community instead suggests that a range of habitats and resources were present, including grass cover that supported the grazing guild; however, the proportion of frugivores indicates that fruiting vegetation was present, as well (Su and Harrison 2007, 2015). Both the overall locomotor and trophic niche profiles are most similar to modern Serengeti woodland habitats (Andrews 1989). In the same location, approximately one million years later, the community structure looks somewhat different, notably in the greater preponderance of terrestrial and grazing species at the expense of browsers and arboreal taxa (Kovarovic et al. 2002). Even when the greater taphonomic loss of small-bodied species in this stratum is taken into account, the large mammal community most closely resembles a semi-arid bushland habitat (Kovarovic et al. 2002). This apparent trend towards increased aridity is also seen elsewhere in the region. Thirty-six kilometers north of Laetoli, where the extensive deposits of Olduvai Gorge record the evolutionary history of hominins in great detail, the 2.0–1.8 Ma Bed I sediments (Deino 2012) indicate a change in climatic conditions towards greater aridity, and the mammal community suggests a shift in the vegetation towards more open habitats at the end of the sequence (Fernandez-Jalvo et al. 1998). However, later in time, the mammalian community structure suggests that even in light of continued increasing aridity (Cerling and Hay 1986), the woody vegetation cover and the mammals it supported had stabilized. Although studies had long acknowledged differences in the Bed II fauna above and below the 1.74 Ma Lemuta Member (Leakey 1971; Hay 1976, 1990; Gentry and Gentry 1978), community structure analyses comparing Lower Bed II, where *Paranthropus* and *Homo habilis* remains have been recorded, to Upper Bed II deposits in which *Paranthropus* persists and *Homo erectus* emerges, demonstrated that the faunal differences are most likely explained by taphonomy; both of the Bed II mammal communities were woodland-adapted (Kovarovic et al. 2013).

Work at Olduvai reminds us that mammal communities vary not only over time, but also over space. A long program of research at the site, particularly in Bed I and lowermost Bed II, has focused on assessing landscape use of resident hominins (Blumeschine and Peters 1998; Blumeschine et al. 2003, 2012a, 2012b), which necessarily considers both habitat and geology. Recursions of the paleo-lake Olduvai and periods where springs and river-fed wetlands were the main water sources shaped the landscape and modified habitat availability intermittently (Ashley et al. 2009; Stanistreet 2012). These hydrological phases would have supported different vegetation complexes across the landscape. A full-scale spatial community structure analysis has yet to be undertaken, but faunal composition does differ spatially (Cushing 2002), and it can be hypothesized that areas of higher relief, where drainage was good and woody growth was possible, supported different communities from those located in areas of poorer drainage with marshy or otherwise more open habitats.

One difficulty in assessing community structure on a landscape scale is that in addition to the fact that mammals are not static users of their habitats and move around considerably, taphonomic conditions may not allow full communities to have been preserved at each place of interest, forcing researchers to "average" the fauna across a large area (see discussion in "Analytical Challenges", below). However, some sites such as Aramis, Ethiopia, where *Ardipithecus ramidus* remains are known at 4.4 Ma, demonstrate that it may be possible to provide a more refined interpretation of community structure variation across a landscape (White et al. 2009). Here, the mammals identified along a 7-km transect situated on a southeasterly gradient vary in their functional adaptions to both the trophic and spatial niche. The entire mammalian community's niche exploitation profile was not considered for both niches, but the selected macromammals studied suggest full community differences between open habitats in the southeast and woodlands, with which *Ardipithecus* is associated, elsewhere.

Analytical Challenges

Locality Size and Habitat Homogeneity

One issue to consider when conducting community structure analysis concerns the size and scale of the areas from which modern faunal communities derive. Very often, they are entire national parks or even entire regions of a country, which are likely to encompass multiple habitat types. This results in faunal lists with species that are not actually found in the same area or habitat in nature but artificially appear on the same faunal list due to the large scale of the faunal survey in question (e.g., Wilson 1975; Happold 1987). This makes it difficult to directly compare fossil and modern faunal communities because fossil sites are often much more constrained in size than the area from which modern comparative faunal communities are derived (Su and Harrison 2007; Louys et al. 2009) and also decreases the resolution of the interpretations possible. Ideally, the geographic scale of the comparative modern communities should match that of the fossil community of interest (Croft 2013).

It is also important to choose modern localities carefully to minimize latitudinal variation and to represent uniform topographical zones and vegetation types (Andrews et al. 1979) although, in theory, the size of the area should not be a significant consideration as long as the habitat is homogeneous across the area covered. The most straightforward way to deal with this issue is to simply avoid faunal communities suspected of representing several major habitat types or to divide them as much as possible according to specific habitats that can be well-defined within the overall area. Alternatively, a statistical approach can be used to identify species lists whose compositions are significantly distinct and under- or over-represent particular species groups. Louys et al. (2009) suggest a taxonomic distinctness analysis based on a measure developed by Warwick and Clarke (1995; Clarke and Warwick 2001) that can determine communities that have a higher than average taxonomic distinctness, potentially the result of sampling multiple habitats across a large area. These can then be excluded from further community analysis since they do represent a natural, habitat-specific fauna.

Defining and Assessing Paleospecies

Although it is not necessary to taxonomically identify individual fossil specimens in a community, discrete taxonomic units still need to be identified. Often material is too fragmentary to allow this, and it is common to see that fossil assemblages have fewer species overall when compared to modern communities (see "Fossil Assemblage Suitability", above); this may relate not only to under-sampling of the fauna generally, but also to an inability to identify all unique paleotaxa. It may be difficult to distinguish between multiple species in a particularly diverse family or tribe with numerous closely-related taxa, with the result that faunal lists may be composed of generic or tribal groups (e.g., "Alcelaphini A" and "Alcelaphini B"). These distinctions may be based on differences in body mass because the morphology is so similar. In such cases, as long as they can be recognized as distinct taxonomic units and ecovariable categories assigned to them, they should be included in the analysis.

Taphonomy and Sampling

There are many taphonomic factors that impact the composition of the final fossil assemblage in such a way that it no longer reflects the composition of the original living community. Most of them involve differential destruction and transportation of bones on the landscape due to fluvial factors, carnivore and rodent activities, weathering, and trampling (e.g., Voorhies 1969a, b; Behrensmeyer 1975; Behrensmeyer and Hill 1980; Blumenschine 1988). Furthermore, collection strategies and/or sampling, regardless of how thorough, are probably not sampling the entirety of what was once the living community. For example, at Laetoli, all specimens identifiable by taxon or anatomical elements are collected (Harrison 2011). This is an intensive collecting strategy that ensures a representative fossil assemblage, but even then, smaller taxa are significantly under-represented. Size-abundance analysis of herbivores >1 kg indicates that species <10 kg are under-represented in the Laetoli fossil assemblage and that the assemblage is taphonomically biased by surface processes (Su 2005). It is important to note that because community structure analysis relies on faunal lists, many of these taphonomic biases are ameliorated and such biases may not need to be corrected prior to conducting an analysis (Andrews et al. 1979). It is, however, useful to identify the taphonomic biases present in the paleontological assemblage of interest for interpreting the results.

Another important taphonomic consideration is the general under-representation of small mammals in fossil assemblages. Although they are useful habitat indicators in their own right and can be subjected to their own community structure analysis to aid paleoecological interpretations (e.g., Reed 2007; Avery 2007; Stoetzel et al. 2011), they present unique challenges to paleoenvironmental inferences based on community structure. They are often accumulated under different taphonomic regimes from the large mammals in fossil assemblages (Andrews 1990a, b; Reed 1997, 2007) or are so poorly preserved that they are under-represented in the fossil community (Andrews et al. 1979; Reed 1997; Su and Harrison 2007). Based on these factors, many researchers make the decision to exclude them from the analysis to reduce the need to consider this taphonomic bias in interpreting results (cutoffs of 500 g, 1 kg, and 4 kg are commonly used; e.g., Reed 1997, 2008; Su and Harrison 2007; Louys et al. 2009; Su 2011, 2016). Where small species are clearly biased in an assemblage, a statistical solution may be to employ a sampling technique that modifies the comparative modern data such that the body mass profiles match that of the target paleontological community (Kovarovic et al. 2013). However, eliminating smaller body mass categories would also eliminate important ecological information, and the analysis would thus be based on a limited array of niches that may not discriminate between different habitats equally well (Mares and Willig 1994).

An isotaphonomic approach can also minimize taphonomic effects (Behrensmeyer et al. 1992). Clyde and Gingerich (1998) only included Paleocene localities in their study of the Bighorn Basin, Wyoming that satisfied several taphonomic criteria (i.e., that sampled the same paleosol facies), to investigate the impact of the latest Paleocene thermal maximum and the earliest Wasatchian immigration event on the local mammalian community structure. Even though this approach may result in fewer localities, it provides some guarantee that any observed faunal changes are not due to taphonomic differences. Indeed, Clyde and Gingerich (1998) were able to demonstrate that short-term climatic change and its associated immigration event had a sudden and long-term effect on the Bighorn community structure.

An important consideration of sampling is stratigraphic control in fossil assemblages. Time-averaging can inflate species richness when taxa that may actually be separated by tens or hundreds of thousands of years are considered to be part of the same community. This creates a problem when comparing with modern assemblages, which are essentially sampling a single point in time. In order to fully appreciate faunal and environmental change through time, it is necessary to have tight stratigraphic control and to sample as small of a temporal unit as possible when conducting community analyses. One of the best examples of this is the examination of faunal and environmental change through the Siwalik Formation of northern Pakistan by Barry et al. (2002). By dividing the five-million-year interval (10.7–5.7 Ma) into 100-Kyr units, they were able to demonstrate a high level of background turnover in the Siwalik record along with brief and irregularly-spaced turnover pulses likely due to climatic and environmental factors. Without this fine-grained control of temporal resolution, it would not have been possible to demonstrate so conclusively the lack of environmental and faunal stasis in the Siwalk record.

Further Considerations and Future Directions

A Dynamic Biome

In community structure analysis and other faunal-based methods of paleoenvironmental reconstruction, we are using ecological information derived from animals as a proxy for the vegetation structure that was present. We are, in effect, assuming that mammalian community structures in similar biomes are convergent regardless of their location in time and space can be distinguished based on the fauna (and their adaptations). However, biomes are dynamic entities, changed by temporal, geographic and scale-dependent events that also change the structure of the associated mammalian communities.

Temporal factors: Temporal changes in the climate and physical environment occur over ecological (days to millennia) and geological (orbital to tectonic) time frames; floral and faunal communities have to adjust to these changes (Overpeck et al. 2003). The circadian response of vegetation to daily differences in the amount of solar energy can be observed as the movement of leaves or the opening and closing of flowers, for example, but it is change that occurs on a longer time scale that can impact on paleoenvironmental reconstruction.

Within decadal and centennial time frames, primary or secondary succession of vegetation alters plant species composition of the biome and, as a result, mammalian community structure. For example, after a disturbance to a forested area, whether by storm, wildfire, or some other event, pioneering species invade the new area quite rapidly and begin a new succession of plants and animals. The animals are often r-selected species early on, but more K-selected animals eventually inhabit the forest as the succession continues (Pianka 1970). Thus, within a relatively short time span, the faunal community structure can change in the same geographic location, and this may impact paleoenvironmental reconstruction.

Climatic events, like ice ages, can cause millennial changes in vegetation (Overpeck et al. 2003; Hessler et al. 2010). Pollen records from both marine and terrestrial sediment cores demonstrate that during the last glacial period, as a result of global temperature change, cold- and warm-adapted plant species altered their distributions (Overpeck et al. 2003; Hessler et al. 2010). As plant composition and the biomes gradually change, mammalian communities respond to these changes by regional- or continental-scale migration, extinction, or by subspecies-level selection (Overpeck et al. 2003), often resulting in a shift in community structure.

Larger changes in biomes occur over geological time scales, both at the orbital and tectonic levels. The orbital level, which spans 10,000 to 100,000 years, includes glacial-interglacial cycles and relates to the orbital forces described by Milankovitch (Ruddiman 2007). These cycles have repeatedly formed and broken up biomes, causing extinction and speciation events in both plant and mammalian communities. Some biomes in the past have no present-day equivalent. Biomes are also affected by plate tectonics and continental drift. These changes take millions of years and cause major changes in biomes by creating new mountain ranges, opening and closing water courses, and altering global climatic conditions. At this scale, mammalian communities can change drastically in species composition and community structure as they are shaped by major extinction and speciation events (Janis 1993).

Geographic factors: Geography is significant for the evolution of biomes and their associated mammalian fauna. Both latitudinal and altitudinal change or the presence of a continental or island environment alter climatic variability and the rate of dispersion and speciation. The amount of solar energy received is directly related to latitude; low and mid-latitudes have high solar radiation and higher latitudes have low solar radiation (Ruddiman 2007). Similar phenomena can be observed with patterns of species richness, which is generally higher in the tropics and lower towards the poles. Several hypotheses have been proposed to explain this pattern, including: (1) warm climates have faster rates of microevolution (Gillman et al. 2009); and (2) the tropics have more energy available in usable form, which results in more organisms and, hence, more species (=species richness-energy hypothesis; Brown 1981). While these have not yet been sufficiently tested, it is clear that latitude and the amount of solar energy have important implications for climate, vegetation and mammalian communities. A similar pattern exists with altitude. Atmospheric temperature decreases by 6.5°C/km as altitude increases (Coe 2009), and this has a significant impact on the vegetation and the associated mammalian community (e.g., Geise et al. 2004).

Other geographical factors such as the size, shape, and type of the observed area (continent or smaller island) also impact vegetation type and structure of the mammalian community. Studies of island biogeography have noted that islands closer to continents have higher species richness than those further away, as they are easier to reach by migrating populations (MacArthur and Wilson 1967). In addition, larger islands have more resources than smaller ones; thus, there is a higher probability of immigration of continental animals (MacArthur and Wilson 1967).

Geographic scale: Changes in vegetation or mammalian communities can also be analyzed at different geographical scales, from the micro- to macro-level. At the macro-level, the analyzed scale is at the continental level where local changes are insignificant from an analytical perspective. For example, as the climate became increasingly arid during the Miocene, grass-dominated open habitats spread while closed forested areas decreased. This had a direct impact on mammalian herbivore tooth structure, which evolved from low-crowned (brachydont) to medium (mesodont) or high-crowned (hypsodont) teeth in response to their changing trophic resources (Eronen et al. 2010a; Strömberg 2011). At the meso-level, changes in vegetation and mammalian communities are observed within continents. A change in climate may cause the disappearance of one biome and the appearance or increase in size of another, as was the case during the late Pleistocene and Holocene, when the same general climatic events affected both South America and Africa. African mammalian communities remained almost unchanged while those of South America changed dramatically (also due in part to human activity; Cione et al. 2003; Barnosky and Lindsey 2010; Barnosky et al. 2016), leading to present-day faunal dissimilarities between the two continents (De Vivo and Carmignotto 2004). At the micro-level, changes in vegetation and mammalian communities are observed in local areas such as a specific island, mountain, valley, or basin. For example, high levels of endemism exist not only in the Philippine islands as a whole, but within individual islands, as well. Repeated rising and falling sea levels during the Pleistocene joined and separated the Philippine islands numerous times, forming the so-called Pleistocene island groups with unique sets of species (Catibog-Singa et al. 2006).

Implications for community structure analysis: Most of the above-mentioned temporal, geographic and scale-dependant events relate to historical contingency, or the effect of the order and timing of past events on community assembly. Abiotic events like wildfires, floods, storms, and earthquakes change species arrival history of a location or area. These biotic events have different priority effects on the order in which species arrive to the primary or secondary succession area. Although quite often the succession may follow an expected order, the consequences of species arrival history can cause differences in the structure of communities, as effects are amplified over time and space via population growth and interactions (Fukami 2015). The results of this are that even in relatively similar environments, faunal composition can be different due to their different histories. This suggests that historical contingency may be an important factor to consider when interpreting the results of community structure analyses (see “Moving Forward” for more discussion and Croft 2006 for a documented example).

Moving Forward

The more nuanced our understanding of the relationship between a biome and its associated mammalian community (and its ecological structure), the better we can infer past environmental and climatic conditions based on proxies. There is much that can be done to refine community structure analyses, thus guaranteeing ever more robust and detailed environmental reconstructions. We suggest that development in the following three areas would be most beneficial to improving the methodology:

(1) **Historical contingency**: As discussed previously, paleoecological studies rely on the assumption of community convergence and, indeed, there are general similarities in community structure between localities of similar latitudes on different continents in tropical and northern (Palearctic and Nearctic) zones. Nevertheless, this apparently only applies to broad locomotor and dietary variables in the tropics (Lintulaakso and Kovarovic 2016) and between extreme environments that are similar, such as desert and steppe communities with high levels of water stress and low complexity in vegetation structure (Rodríguez at al. 2006). Historical effects are likely to be responsible for demonstrated differences between communities in similar habitats (Losos 1996; Rodríguez et al. 2006; Graham and Fine 2008; Fukami 2015; Lintulaasko and Kovarovic 2016), but it is not yet clear how historical contingency impacts the application of community structure analysis to paleoenvironmental reconstruction or how frequently we may simply be analyzing environments for which there are no modern analogs (Soligo and Andrews 2005; Semken et al. 2010). Thus, a better understanding of the effects of historical contingency should be considered as one of the next steps in improving the method.

(2) **Heterogeneous paleoenvironments**: Community structure analysis is an excellent way of reconstructing the spatial and trophic niches that were available to past communities. But, it can be a coarse approximation that forces habitats into discrete and broadly-defined categories, glossing over the nuanced differences among them (regardless of the mechanisms that are responsible for them). Steps are being taken to move away from categorical habitats and environments, with greater emphasis placed on the multidimensional spectrum of many environments. Louys et al. (2015) outlined techniques for describing habitats and environments using a number of biotic and abiotic quantitative variables. They calculated arboreal heterogeneity of a particular locality in terms of the proportions of heavy, moderate, light, and absent tree canopy cover to reconstruct the paleoenvironment (Louys et al. 2015). The incorporation of a continuous multidimensional spectrum of environmental conditions rather than a simplistic partitioning of habitats into categories will be essential forproviding a more nuanced and accurate reconstruction of

paleoenvironment and a better understanding of the relationship between the biome and their associated faunal communities.

(3) **Paleoclimate reconstructions**: The method as it is generally applied also lacks the ability to clearly identify paleoclimatic factors, focusing largely on a reconstruction of the physical environment rather than climate. However, the use of averages of ecometric traits (species traits that are easily measurable, whose structure is closely related to their function, and whose function interacts directly with local environment) in communities has been shown to be connected to precise measures of climate variables, such as the amount of precipitation or temperature (Eronen et al. 2010b; Fortelius et al. 2016; Žliobaitė et al. 2016). These types of data allow us to characterize physical habitats at the regional scale, linking them specifically to primary production (Fortelius et al. 2016).

Community structure analysis is rooted in the niche concept and the idea that faunal communities and the adaptations of their members can provide information about their environment. It is a powerful tool for reconstructing paleoenvironments. While it does not rely on a single mammalian taxon, it does incorporate ecometrics and taxon-specific analyses (dietary and locomotor reconstructions for specific taxa) to arrive at a holistic and community-level perspective on paleoenvironmental reconstruction. With further development and refinement, this methodology can help move us away from categorical descriptions of paleoenvironments and emphasize the continuous nature of ecological variables. This will allow for more nuanced reconstructions of paleoenvironments and a better understanding of the relationship between biotic communities and their environments.

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