# Taxon-free methods of palaeoecology

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Four types of taxon-free analysis of mammalian faunas are discussed to come to an understanding of the degree to which they are independent of taxonomy. Species richness patterns and size distributions of faunal assemblages provide general indications of palaeoecology and are based entirely on species identifications; ecomorphology targets specific taxonomic groups, but within the group it is partly independent of taxonomy; community ecology describes mammalian communities by their levels of diversity within distinct ecological categories rather than by their species, and two approaches are based either on qualitative evidence (ecological diversity) or on quantitative evidence, combining ecomorphological data for whole communities (community ecomorphology). No method is entirely taxon-free, but all have stronger ecological foundations than methods based on linking fossil species of unknown habitat with their supposed habitats based on their relationships with their living relatives.

## Introduction

Over the past 40–50 years there has been an explosion of approaches to reconstructing the palaeoecology of fossil species and reconstructing terrestrial habitats in the past. Methods developed are often specific to particular taxa, but in recent years there has been more of an emphasis on taxon-independent or taxon-free approaches. The argument runs that fossil species, being for the most part extinct, have unknown ecologies and therefore cannot form the basis for reconstruction of past habitats. Sources of evidence in place of taxonomic identifications have included distributions of species richness, species sizes, functional morphology (the basis for ecomorphology) and community ecology. Some of these methods have recently been reviewed by Reed

(2013), and they are taxon-free to a certain extent, but as they are often limited to use in a specific group possessing particular adaptations, the methods are taxon-free only when restricted to specific and predetermined taxonomic groups (for example in families such as Bovidae).

The issue comes down to the ecological information inherent in species identities: living species have known ecological ranges, and their place in living communities can be observed at first hand. There is, however, one source of evidence for fossil species, whether extinct or extant, that provides first-hand evidence of their ecology, and this comes from stable isotopes preserved in their bones and teeth. The analysis of carbon isotopes preserved in the teeth of mammals measures proportions of $^{13}C/^{12}C$ ($\delta C$), and this relates to proportions of $C_3$ to $C_4$ plants

present in the diet of the animals. In tropical environments, $C_3$ plants include nearly all trees, shrubs and herbs, together with grasses where there is a cool growing season, while $C_4$ grasses grow in open, unshaded places. An animal eating mainly grass in open habitats will have $C_4$ enamel, and an animal eating mainly leaves from trees and bushes will have $C_3$ enamel, and this applies in the same fashion to all mammals, regardless of their taxonomic affinities. Kingston (2010) examined over five hundred specimens from the Pliocene deposits at Laetoli and found a mix of $C_3$ and $C_4$ signals on the teeth from twenty three large mammal species, some of which could be shown to be browsers, some grazers, and some in between. The results show great variability in the environment at Laetoli, with vegetation varied enough to support the extremes of grass to leaf eaters (Kingston & Harrison 2007).

Kingston (2010) also investigated oxygen isotopes at Laetoli to calculate an aridity index for the site derived from the water deficit (WD) calculated for different groups of mammal. He found the range of values for WD at Laetoli indicated mean annual precipitation nearly the same as it is today.

Similar work at a Miocene site investigated the carbon isotopes preserved in the teeth of sixteen species of herbivore and carnivore from Paşalar, Turkey (Quade *et al.* 1995). The sixteen species showed a range of palaeodiets from strongly $C_3$ to intermediate $C_3$ with $C_4$. This indicates that the area was well wooded but included some open areas. The oxygen isotopes in the tooth enamel was greatest in the giraffids, which feed on the tops of trees where the canopies are exposed to light, and the bovid with the highest $\delta^{13}C$ values also had values similar to the giraffe, indicating it was a grazer feeding in open habitats. In contrast to these species, most of the other animals tested in the Paşalar fauna had lower carbon and oxygen values, indicating they were feeding on $C_3$ vegetation and drinking environmental water.

Nitrogen isotopes are also analyzed to investigate differences in trophic level, which may indicate the presence of meat in diets of fossil animals or the consumption by herbivores of aquatic plants (Palmqvist *et al.* 2008). The $\delta^{15}N$

levels distinguish meat-eaters and herbivores, but since many 'carnivorous' species also eat a lot of vegetation, the question arises as to how much meat is needed to produce a meat signal with nitrogen isotopes. This is particularly controversial at present concerning the diet of cave bears (*Ursus spelaeus*), with some isotope studies showing it to be entirely herbivorous and others showing an element of carnivory (Figueirido *et al.* 2009). When meat-eating populations of chimpanzees have been investigated, no difference in isotope values has been observed between male and female chimpanzees despite the fact that the males have been observed to eat six or seven times the quantity of meat than females (Smith *et al.* 2010). The explanation for this might be that the tooth enamel, which is the tissue that is isotopically analyzed, is formed during infancy, and infants and juveniles almost never are allowed to share meat. Another explanation may be that the adults do not eat enough meat to affect their isotopic signal.

These examples show how the ecological place of some fossil species may be identified and how this may provide information directly on the environment. Although taxonomic designations have been used in interpreting the results, these are not necessary. All that is necessary to know is that there are *x* numbers of browsers, *y* numbers of grazers, and *z* numbers of carnivores, and the actual species to which these characteristics attach do not need to be known in order to formulate a reconstruction of the habitat occupied by the assemblage. There are limitations to this type of analysis, however, for the distinction between $C_3$ and $C_4$ photosynthetic pathways is only useful after the spread of $C_4$ grasses, and there are complications in interpretation in wet environments (Palmqvist *et al.* 2008).

We are now going to look at several other ways of reconstructing habitat, for some of which Mikael Fortelius has been the leading light. One is to look at species diversity (richness) in a fossil fauna, and, taking taphonomic considerations into account, this may provide some information on palaeoecology. Another method examines the morphological adaptations and body size distributions of fossil species in relation to their probable functional morphologies, that is their ecomorphology. Thirdly, we

will consider briefly the issue of community ecology and how it may be integrated with ecomorphology. The question we address for all of these methods is the extent to which they can be considered independent of taxonomy.

## Species diversity

In 1955, Shotwell compared numbers of specimens with numbers of individuals in fossil faunas to arrive at an estimation of the proximity of different types of mammal to their place of preservation. He predicted that these estimations would exclude volant and arboreal species, and he further predicted that a point is reached "at which the average number of specimens per individual [shows] … the limit of the proximal community", and that mammals whose community in life is close to the site of preservation are likely to be more completely represented. Finally, communities represented at a fossil site other than the proximal one must be derived from a habitat present somewhere in the region. This method operates independently of taxonomy in some measure (Shotwell 1955). For example, Shotwell applied this methodology to a mid-Pliocene site in Oregon (Shotwell 1958), and based on relative abundances of mammal species he showed the presence of three communities from three major habitats. Although this methodology is based on taxa, it opened the way to a new approach to palaeoecology that is still being explored today.

Wolff (1975) added the analysis of species richness ($\alpha$-diversity) to the equation, combining it with Shotwell's data on species abundance. Like Shotwell (1955), Wolff was concerned about sample size, an important element in the ecological analysis of fossil faunas and now sadly neglected, and he found, for example, that something close to the expected number of species in a region was only reached after sampling two large localities of 800 (identifiable) specimens each. Such numbers are easily reached during surface collections, but excavation sites generally have to be large to achieve such numbers, particularly for large mammals, which in any case are much less abundant regionally than small mammals.

These early publications were based on taxonomic identifications both to estimate species richness and species abundance. Most early direct attempts to reconstruct palaeoecology were also based on species identifications, equating the ecology of fossil species with that of their living relatives (for example Andrews & Van Couvering 1975). Species richness of mammals in Africa has also been related directly to climate, and different patterns emerged; for example, arboreal frugivores were most highly correlated with annual rainfall, low seasonality and forest vegetation. Terrestrial browsing herbivores on the other hand had distributions less related to rainfall and more to areas of topographic change. No group of mammals within tropical and subtropical Africa was correlated strongly with temperature, whether mean temperature or seasonal variations, although large mammals were weakly correlated with minimum monthly temperature in southern Africa (Andrews & O'Brien 2000). In other words, different groups of animals each tell their own story as regards their preferred environments, and it is unrealistic to apply the same ecological criteria to each (Andrews & O'Brien 2000). This kind of analysis can be applied to fossil assemblages where it is possible to assign ecological parameters to the fossil species, but confounding issues include sample size, species equability, size of area sampled and the length of time represented by the assemblage.

Species numbers in relation to (marine) environments has been related to time (Boucot 1978) in identifying niche partitioning, indicating a relatively unchanging carrying capacity of species communities. Damuth (1987) used a similar argument for land mammals, showing that population energy use is approximately independent of body mass over a range spanning more than 11 orders of magnitude. He showed that this principle holds when data are broken down into regional or single communities, and this appears to be a widespread rule of animal ecology and community structure arising from energetic and metabolic regularities in community structure (Damuth 1982). Based on this conclusion, Soligo (Soligo & Andrews 2005) constructed ranges of variation for living mammal communities, showing high levels of consistency in

the distributions of mammal communities across geographical and ecological ranges. These were analyzed by size category and trophic niche and broken down into ten functional groups, and he used these to show the patterns present in living mammal communities across a wide spectrum of climate and habitat. These patterns then formed a base line for fossil faunas, seeing whether they fell within the limits of modern faunas (Soligo & Andrews 2005). This method is totally independent of taxonomy, but what it measures is divergence of fossil faunas from the universal principle of community structure as proposed by Damuth (1987), which applies across all living mammal communities and all habitats. As such, it does not identify specific habitat patterns, only divergence from them, usually as a result of taphonomic bias in the fossil record (Soligo & Andrews 2005).

The existence of diversity patterns across habitats and through time is an interesting phenomenon, for it suggests finite limits to mammalian variation. Werdelin and Wesley-Hunt (2010) showed that other factors may be involved, for carnivore disparity (or morphological diversity, which they show is independent of taxonomic diversity) is also remarkably uniform across continents and habitats. They conclude that this may be a pattern inherent to carnivorans, but it may be that it is a feature of mammal communities generally, as suggested by the energetic and metabolic constraints of mammals described above (Damuth 1987).

## Ecomorphology

Ecomorphology of mammals examines the functional morphology of animals in a fossil fauna in relation to the environment. By comparing the pattern of morphologies present in a fauna with the patterns observed in recent species of known habitats, inferences are drawn about the range of probable adaptations present in the fossils. The theoretical basis for these inferences is derived from the observation that mammal species occupying similar habitats across the world tend to show parallel or convergent adaptations (Darwin 1859). Convergent evolution results in the production of similar adaptations in phylogenetically

unrelated organisms that are subject to similar agents of natural selection, although convergence is constrained by availability of genetic variability in the converging lineages and sufficient time for it to act. For example, lowland tropical forests in Asia, America and Africa share rodents with gliding (flying) adaptations belonging to different families, Anomaluridae and Sciuridae, not to mention gliding marsupials in Australia; they also share rodents and insectivores with squirrel-like scansorial adaptations and primates with grasping feet adapted for life in trees. Sloth-like arboreal species such as Bradypodidae in South America and Manidae in Africa and Asia have similar habits and diet; the New World monkeys, Platyrrhini, show many similar adaptations to life in trees to the Old World Catarrhini, even though the two suborders diverged at least 40 million years ago; and the anteaters such as Myrmecophagidae in South America and Tubulidentates in Africa show remarkable convergence. These are the extreme examples, but it is also evident that there is considerable intercontinental similarity at what can be called the cumulative niche level, for example in numbers of frugivorous mammals in the trophic niche, or arboreal mammals in the spatial niche (Harrison 1952, Clutton-Brock & Harvey 1977).

The most obvious of ecomorphological characters is body size. Figure 1 shows the species richness for nine modern faunas, and while there are differences within and between habitat types there is no clear overall trend. As one element of the cumulative niche, body size has some relevance, but on its own it is not diagnostic of ecological or biogeographic boundaries. In addition, the estimation of body weight for fossil animals necessarily requires some taxonomic basis, for weights are predicted on the basis of regressions of some skeletal element against body weight, and these are usually calculated within some higher order taxonomic grouping, e.g. family for Bovidae, order for Primates.

Most ecomorphological studies have been aimed at specific parts of the skeleton, for example microwear on teeth (*see* Walker *et al.* 1978). They showed that "Microwear details on teeth of two sympatric species of hyrax are correlated with major dietary differences". They were able to distinguish between grazing and browsing
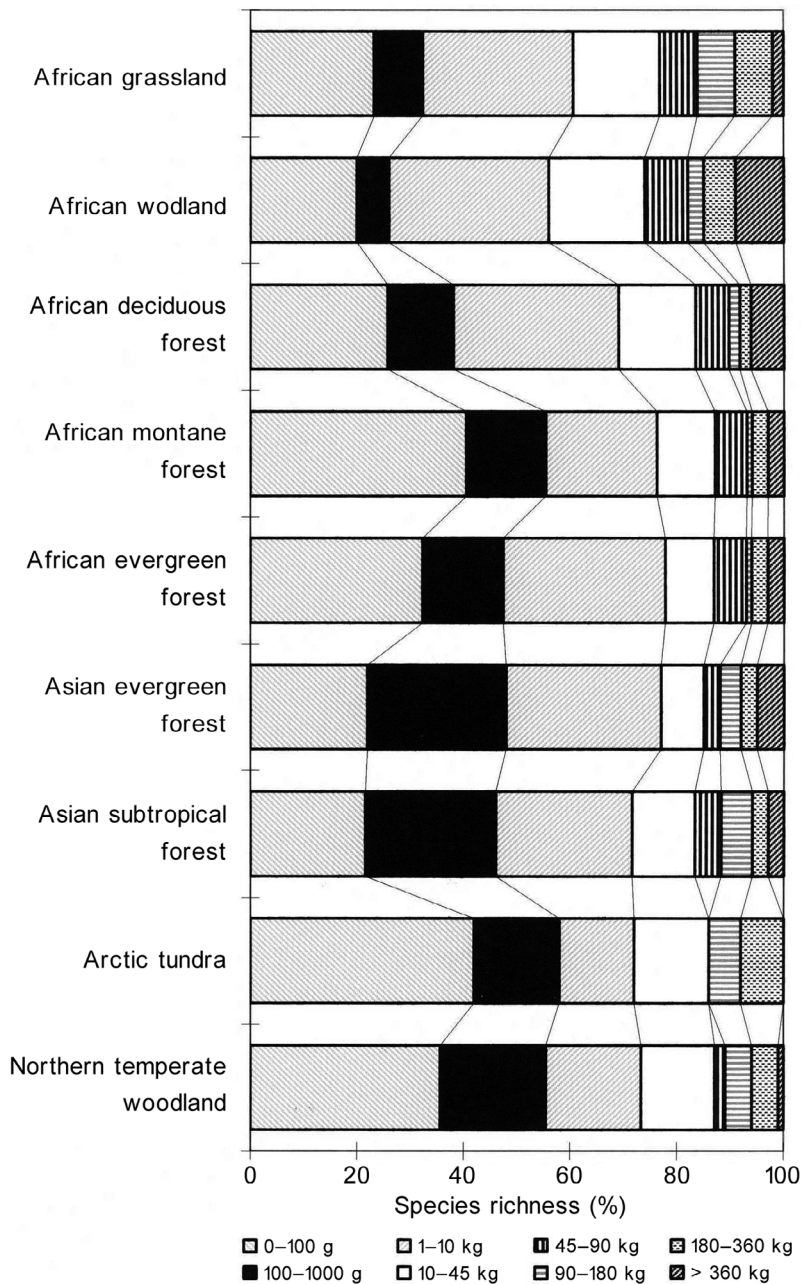
**Fig. 1.** Species richness in nine modern habitat types. Small mammals are most abundant in tropical forest, arctic tundra and temperate woodlands, where medium-sized mammals (1–10 kg) are least frequent. In African grassland and woodland habitats large mammals are never frequent, but mammals over 45 kg are most frequent.

modifications, although they pointed out that the reconstructed diet from microwear applied only to the period shortly before death. In the same paper, incidentally, Walker *et al.* (1978) also investigated phytoliths, finding abundant but unidentified phytoliths on the teeth of the grazing species.

There are two questions concerning ecomorphology: is it really taxon-free when most analyses target specific taxonomic groups (most commonly bovids)? and is there any common ground between families such that their adaptations or ecomorphologies can be interpreted in the same way? (for example between bovids and equids). Adaptations of the femur for running in carnivorans are not the same as the adaptations for the same behaviour in equids, and they are different

again in bovids. As a result, the selected skeletal elements to be analysed must first be assigned to a taxonomic group, and comparisons with fossil bones can only be made within the same group: bovids with bovids, suids with suids, and so on. This leads to the further question: can we remove taxonomy when we are looking at adaptations that are linked to that group's ability to succeed in that environment?

An example of the kind of pitfall when taxonomic differences are not taken into account is provided by Harvey and Pagel (1991). Hawks, shrikes and Australian shrike tits have similarly hooked beaks, which might be taken to indicate similar diets in all three, but whereas the first two feed on small mammals, using their hooked beaks to tear open their prey, the shrike tits feed on tiny insects which they eat whole. What they use their beaks for is to rip bark off trees to get to the insects rather than directly on their prey, so although the function of the beak is the same, to tear and rend, its application is different. This example could be extended to other species with hooked beaks, such as owls, that swallow prey whole, or to parrots and lovebirds, that use their beaks to open up fruit.

The strength of ecomorphology as a method of palaeoenvironmental reconstruction is that it is quantifiable. Measurements can be taken on different parts of animal skeletons or teeth and compared with those of other skeletal elements and teeth. For example, cursorial bovids that live in open habitats have a laterally expanded femoral head, whereas forest bovids, which leap more than they run, have a more spherical head giving greater ranges of movement, and these shape differences can easily be quantified (Kappelman 1991). Is the same level of difference seen in equids and rhinocerotids (cursorial), cervids and carnivores (leaping)? Large parts of the skeleton of 59 species of equid, suid, camelid, tragulid, cervid, giraffid and bovid were investigated by Köhler (1993), and she identified ecomorphological characters crossing taxonomic boundaries, such as the cervid/bovid femur, equid/bovid/camelid metacarpus, bovid/equid limb proportions, and many others. On the basis of these similarities, she defined morphological types based on analyses of body profile, horn types, upper and lower jaws, morphology of the limb

extremities, and proportions of the limb bones and combinations of species with similar adaptations were taken to indicate palaeoenvironments.

On the other hand, a quite different suite of characters was used by Valkenburgh (1987) to distinguish between adaptations in climbing, digging and running (cursorial) carnivores, and these characters are good predictors of locomotor behaviour in living carnivores. For example, arboreal carnivores have more strongly curved claws, shorter metatarsals and longer proximal phalanges than do terrestrial species. More recent studies have investigated the ecomorphology of additional body parts: phalanges, astragali and radii of bovids (Bishop 1999); nine types of skeletal element of bovids (Kovarovic & Andrews 2007, 2011, Kovarovic *et al*. 2002); and degree of hypsodonty of the bovid molars (Fortelius 1985, Fortelius *et al*. 2002, 2003).

Hypsodonty is a measure of how high the crowns are on mammal teeth, and generally speaking, the higher the crown the longer the effective life of the tooth for animals feeding on abrasive material (Janis 1988, 1989, Janis & Fortelius 1988, Jernvall & Fortelius 2002). For example, herbivores feeding in open habitats have significantly more hypsodont teeth (regardless of food preference) than ungulates living in closed habitats. This has been taken further by Damuth and Janis (2011) by linking variation in hypsodonty not only with food type but with amount of soil ingested during feeding, and the link with food occurs because grazers feed in open habitats and their food source is close to the ground. Browsing herbivores, by contrast, feed on leaves of trees or bushes well above ground level. This can create problems, for they show that the pronghorn antelope (*Antilocapra americana*) has highly hypsodont teeth but it eats little grass. This anomaly has often been interpreted as an evolutionary hold-over from a time in the past when it did eat grass, but Damuth and Janis (2011) showed that a confounding factor is the presence of soil grit in its food.

Mikael Fortelius and colleagues make use of degrees of hypsodonty as a proxy for degrees of aridity in European and Asian faunas (Fortelius *et al*. 2002, 2003). They show that there is a relationship between hypsodonty and rainfall at the present time, that predicted rain-

fall based on hypsodonty is concordant with other climatic evidence, and that changes in climate, for example between the north and south sides of the Tibetan plateau, are reflected in changes in hypsodonty in herbivorous mammals. Based on these observations, they have been able to plot maps of past rainfall throughout the Miocene (Eronen *et al.* 2010a, 2010b). Jernvall and Fortelius (2002) also found that only the commonly found mammals show increases in hypsodonty during the Miocene, so it is only they that have been able to expand their range in response to drying conditions. When fossil primate distributions are compared against the past rainfall maps, Eronen and Rook (2004) could then show that the primate sites are found within humid areas of Europe and Asia in contrast to non-primate sites which have a broader spectrum of habitat type. Moreover, as climates deteriorated during the Miocene, fossil apes in particular became more and more restricted to humid areas until eventually disappearing.

In another ground-breaking study, Palmqvist *et al.* (2008) combined measures of hypsodonty with evidence from stable isotopes on an early Pleistocene large mammal fauna from Venta Micena in Spain. The hypsodonty index indicated that seven herbivores had grazing adaptations, two were mixed feeders, and two were browsers, but when the carbon isotopes present in their teeth were analysed, it was found that all 11 species consumed exclusively $C_3$ vegetation (Palmqvist *et al.* 2008). Differences in their oxygen and nitrogen isotopes revealed further differences in uptake of water or consumption of aquatic plants, showing that it is possible to reconstruct some elements of past behaviour and trophic patterns.

Studies on the shearing or blade-like morphology of teeth have been related to different food types, so that teeth with sharp blades producing a high degree of shear tear open tough food like grass. By contrast, food that is abrasive, but brittle rather than tough, is associated with more flattened crowns, so that blades are not needed for its comminution. Animals with ridged teeth, such as the bilophodont teeth in monkeys, is commonly related to diets consisting of tough and abrasive foods, and this is the major distinguishing point between monkeys and

apes at the time of their divergence, apes retaining primitively flat crowned teeth (Kay 1975, 1977, Kay & Hiiemae 1974). Similarly, Hunter and Fortelius (1994) showed dietary differences in two closely related suid species that can be related directly to the differences in development of bilophodonty on their molar teeth.

Quantitative analyses of tooth wear have also proved valuable as another ecomorphological method for reconstructing diets in fossil mammals. Early work measured gross differences between grazers and browsers, but increasingly refined methods have led to greater distinctions being made, in particular relating to frugivory. Gross wear patterns have sometimes been used to estimate diet, particularly for example the wear gradient, or difference in degrees of wear between anterior and posterior molars, but recent developments have been in the analysis of mesowear and microwear (Fortelius & Solounias 2000). The former measures the heights and shapes of cusps and the degrees by which they rise above the valleys between them; and microwear measures the sizes and depths of microscopic scratches and pits on the surfaces of the teeth. The two methods of analysis complement each other, for while the former provides long term dietary signals through the life of the individual, the latter provides dietary information shortly before the death of the individual, for microwear traces are quickly obliterated by subsequent meals.

Study of mesowear readily distinguishes between browsers (leaf-eaters) and grazers (grass-eaters), with intermediate categories as well. The method was extended to horses by Kaiser and Fortelius (2003) and later on to primates (Deane 2009), particularly the differences between cercopithecine and colobine monkeys. Incisor morphology in primates can also be related to diet, and it has long been known that frugivorous species have relatively larger incisors than leaf-eating species, particularly marked when colobine monkeys are compared with cercopithecines. The same difference is seen when gorillas are compared with chimpanzees and orangutans. Within the frugivores, hard object fruit-eaters have more strongly curved incisors, both side to side and from top to bottom, while soft object fruit-eaters have less curved incisors.

Leaf-eating primates have the flattest incisors, and the spectrum of differences in living primates is similar to that seen in Miocene apes.

There is also a relationship between brain size and diet, or more specifically between brain size and foraging strategies (Mace *et al.* 1980). Can brain size therefore be regarded as an ecomorphological variable? The answer is probably yes, although no studies have investigated this relationship in detail. Mammals feeding on dispersed food items such as insects or fruit have relatively larger brains, and there are interrelationships between brain size, diet and locomotion, for example fossorial species feeding on roots and tubers having smaller brains than those feeding on insects. Similarly there is some indication that some arboreal or aquatic species have a relatively larger brain than terrestrial forms. These relationships are not simple, however, for brain size is also dependent on high quality diets, such as fruit or animal matter (Milton and May 1984), and conversely it may relate to basal metabolic rate (Martin 1976). Increase in brain size has been seen to be related to changing diets in humans (Aiello & Wheeler 1995); it was argued that the great increase in brain size during human evolution was an 'expensive' adaptation that could only be paid for by a dietary shift to high quality food items, which in the case of human evolution was the change from herbivory to carnivory (Aiello & Wheeler 1995). This idea was extended further by Wrangham (2009), who proposed that the growth of meat eating was followed closely by the development and control of fire for cooking. Cooking both meat and vegetable foods increases the calorific value of the food, makes it easier (softer) to eat and makes it more digestible, compensating for the expense of increased brain size.

The link between microwear and diet was developed by Butler (1952). Since then, numerous studies have established it as a means of identifying diet, although it may be an ephemeral phenomenon only recording diet for the last few meals of an animal's life. The use of scanning electron microscopy was crucial to the development of the method (Walker 1981, Walker *et al.* 1978). The field was systematized by the work of Ungar (2007, 2009, Ungar & Kay 1995) and by Teaford (1988, 1991, 1994). The significance of grit or dust particles taken up with food items has been described by Ungar (2009) and more particularly by Damuth and Janis (2011) and Strait *et al.* (2012). More recently, Scott *et al.* (2012) isolated four microwear parameters and analyzed a range of living monkeys and apes, confirming that microwear textures vary with diet in primates. These have the potential to discriminate the diets of fossil primates, but in a recent study it has been shown that most plant remains have little impact on the formation of microwear features (Lucas *et al.* 2013). They showed that macroscopic plant remains, even hard shells and seeds, have only about 10% of the hardness of enamel and therefore are not sufficiently hard to scratch surface enamel. They conclude that it is dust ingested with food that is likely to be the cause of many microwear features, and over time they may even obliterate deeper scratches and gouges formed when soil grid is ingested with underground or close-to-the ground food items (Lucas *et al.* 2013).

Both dietary and locomotor adaptations have been combined in some palaeoecological analyses, for example the analysis of carnivore faunas by Marean (1989). Sabertooth cats were compared with modern felids and found to be ecologically distinct. Sabertooth incisor and carnassial morphology indicate extreme flesh specialization but lack of bone crushing ability, while their postcranial adaptations indicate noncursorial leaping modifications. This is taken to imply a distinct carnivore community in the past that was dominated by sabertooth cats in closed habitats, although Palmqvist *et al.* (2008) showed that while some of these hypercarnivores preyed on ungulates adapted for closed habitats, others included prey from open habitats. This reflects likely resource partitioning among sympatric hypercarnivores in the early Pleistocene, and there was almost certainly considerable overlap with other large carnivores (L. Werdelin pers. comm.).

## Community ecology

In community analysis, mammalian communities are described not by their taxonomic content but by their levels of diversity within distinct
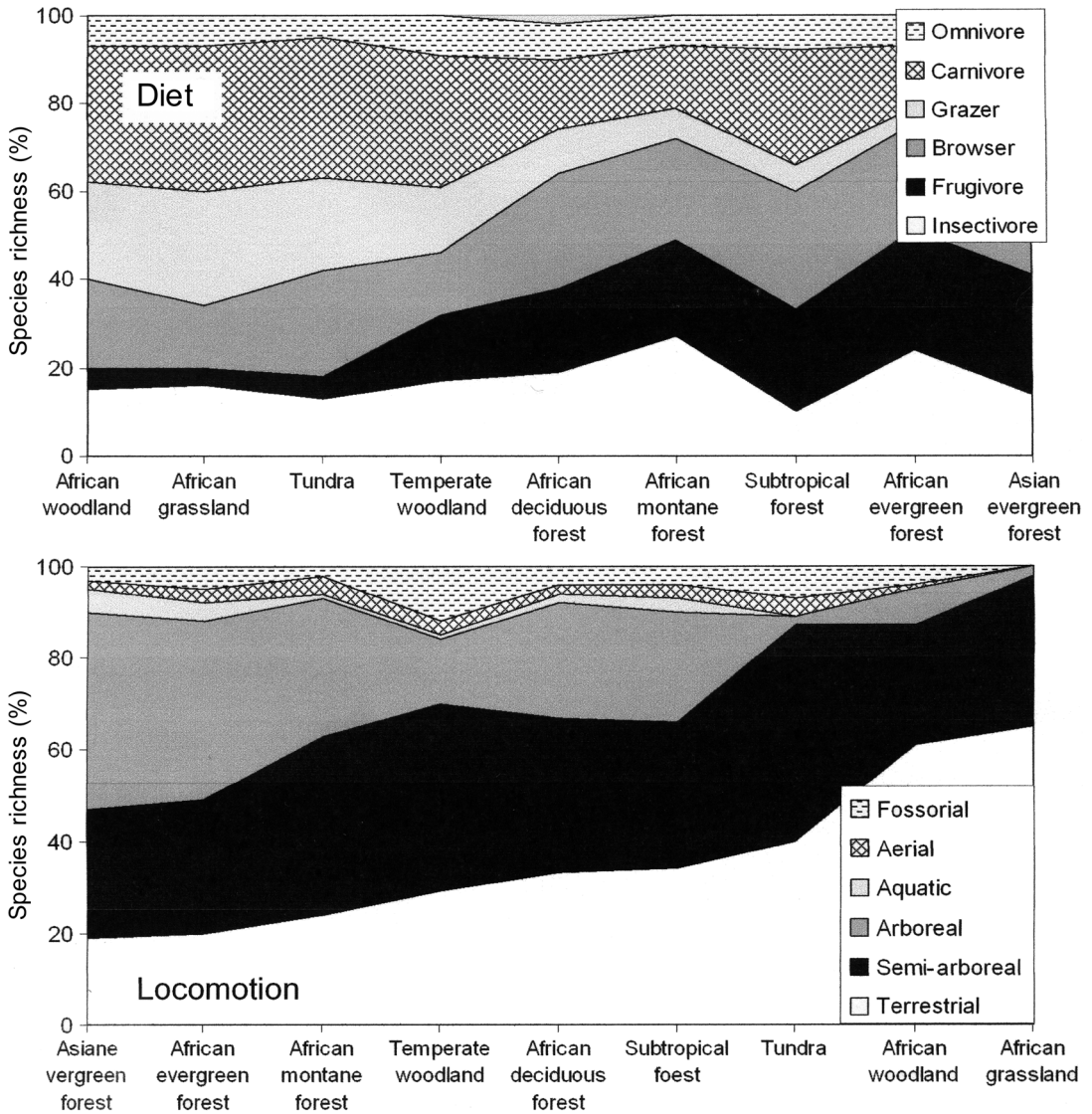
**Fig. 2.** Distributions of dietary and locomotor adaptations in nine modern habitat types. The dietary distribution is set out with the lowest frugivore and insectivore distributions on the left of the figure, with browsing herbivores also increasing from left to right and grazing herbivores decreasing. The locomotor distribution is set out with the lowest terrestrial highest arboreal distributions on the left. (Arboreal in this case includes both strictly arboreal and scansorial mammals.)

ecological categories. There are three aspects of mammalian populations which can be identified in fossil mammals and which relate to their ecological niche: their body size (already mentioned above), the space they occupy, and their trophic level, so that for any one mammal species, the combination of these three sources of information goes a long way towards distinguishing the ecological niche which it occupies and to which

it may be more or less adapted. The combination of these data for all the mammals in a fossil mammalian community can therefore be taken to indicate the range of ecological niches occupied by that community, and hence to define the ecological diversity of the community (Fig. 2). The interactions of the faunal elements making up a community (i.e. its trophic structure) define the limits of the community, both geographi-

cally and temporally, and these may change with time by what Olson called community evolution (Olson 1980), although this is better seen as community succession in the sense of Shotwell (1964).

Ecological diversity was derived from observations made on living faunas by Harrison (1962) and Fleming (1973). They showed that at the present time, the latitudinal changes in species diversity, and their size, spatial and trophic relationships, were largely due to southward increase in number of bat species. When fossil faunas were examined, bats had to be omitted because they are so scarce in mammalian fossil faunas, but the ecological variables could be estimated from the morphologies of the fossil mammals: size by regressions of skeletal elements on body weight, spatial adaptations by morphologies of the limb bones, and trophic adaptations by the teeth (Andrews *et al*. 1979). As for ecomorphology, the regressions and comparisons are made within taxonomic groupings, and to this extent they are not taxon-free, and moreover the ecological assessments of the spatial and trophic adaptations are based on qualitative, not quantitative data. This method, however, took into account entire communities of mammals as opposed to what was deemed to be 'significant' parts of it (Gagnon 1997, Reed 1997). The method has been applied as far back as the Eocene (Collinson & Hooker 1987, 1991, 2003), showing the presence of evergreen forest in southern England in the Eocene. Similarly, an analysis of a series of sequential faunas from Olduvai Bed I (Fernandez-Jalvo *et al*. 1998) showed that the proportions of frugivores, browsing herbivores and arboreal mammals changed from showing dense woodland immediately above tuff 1B and associated with *Zinjanthropus boisei* to more open woodland above tuff 1D, with the loss of the arboreal species, reduction in frugivore species and the first appearance of *Homo habilis*.

## Community ecomorphology

In order to make comparisons within and among habitats, the ecological adaptations demonstrated by ecomorphology are best analysed at the com-

munity level. For this to happen, however, it is necessary to show that the same set of measurements can be used both on different taxonomic groups and on modern and fossil assemblages. Hixson (1998) attempted to demonstrate this based on the 23 modern faunas analysed by Andrews *et al*. (1979) and 27 measurements from 92 species of mammalian ecomorphologies identified for specific taxa (Jenkins & Camazine 1977, Jouffroy & Lessertisseur 1979, Aiello 1981, Scott 1983, 1985, Van Valkenburgh 1985, 1987, Kappelmann 1986, Anemone 1993, Kohler 1993). The same sets of measurements were obtained for all taxa, regardless of taxonomy, with the aim of testing whether they could be applied across some or all family groups and whether all ecomorphological data for entire faunas might produce patterns that distinguish, for example, a woodland fauna from a forest fauna. Fossil postcrania are often identified to family level only and this study demonstrates that a method of community analysis that relies on postcranial measurements alone can give good results.

A consequence of combining many phylogenetically distinct taxa is that it limits the number of niche-related variables to those that are consistent with the morphologies of all the species being used in the analysis. While postcranial material is similar and adapts somewhat similarly to space-use pressures, cranio-dental morphology does not. It is hard to devise dental ecomorphologies that provide information that is more informative than those used within taxonomic groups for the reconstruction of habitat (the exception to this is isotope data). This is because a wide variety of food types can be found in overlapping or even dramatically different habitats; for example, meat is as available to carnivores in forest habitats as it is in grassland. Grass is prevalent in wooded areas as well as in grassland, and browse can be found in all habitats except grassland. This means that while it seems as if more information will come from an analysis that includes size, space use and trophic level, when using ecomorphological data, trophic level and space use might produce opposing signals.

Principal components analysis (PCA) of the complete set of 92 mammal species showed that

**Fig. 3.** The total two-dimensional space occupied by 89 species in the 23 faunas examined. It is based on PCA of 18 eco-morphological indices for all taxonomic groups. Individual plots for each fauna were not distinctive for habitat type. ◆ Perissodactyla, ■ Primates, ◄ non-bovid Artiodactyla, ▲ Carnivora, ● Bovidae.
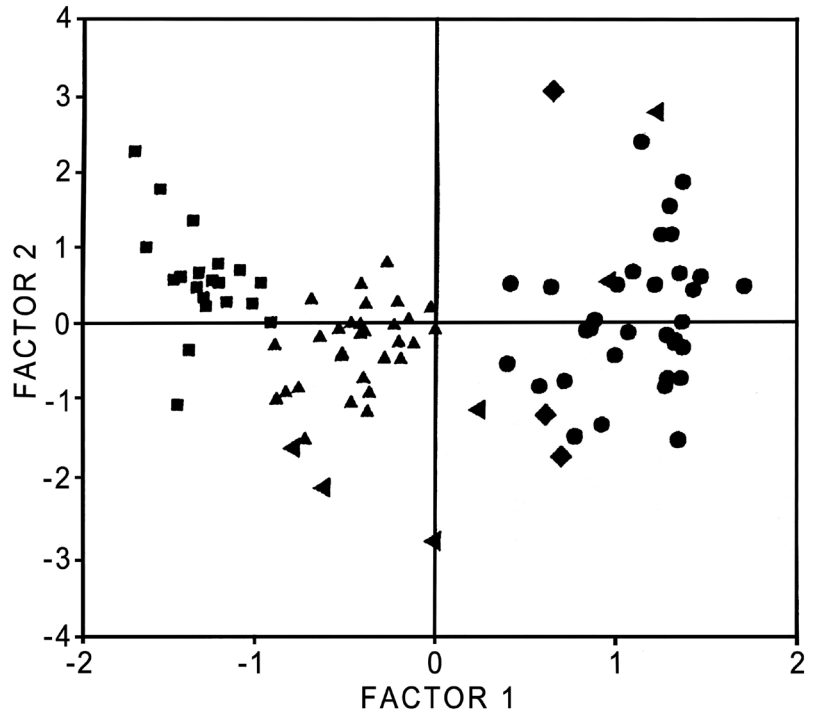
the discrimination was much reduced when all taxa were considered simultaneously. There was no clear pattern differentiating between species from different habitat types and when the 23 mammal faunas were examined, morphological space was similar for every habitat type (Fig. 3). This suggests that another factor is driving this distribution and the other major factor, the one we are trying to remove in a taxon-free method, is phylogeny. When each taxonomic group was looked at separately it is apparent that within each of carnivores, artiodactyls, perissodactyls and primates there was a general separation into more open and closed habitats, but the bigger differences between taxonomic groups is what is driving the overall pattern. There was little overlap between taxonomic groups with this data set (Fig. 3).

Second PCA on the data set, using the same data as above, but analysing higher order taxonomic groups separately (primates, bovids, non-bovid artiodactyls, carnivores and perissodactyls), provided better separation between species from different habitats. The problem then becomes how to use this information in an additive way to recombine the faunas. This was done

by creating a plot of the total ecomorphological space for each fauna by superimposing the separate results into a combined plot using the first two components from five analyses (Fig. 4). This provides a depiction of the total morphological space and visually describes the space use distribution of the 92 species, but it is not valid to draw ecological conclusions from the variables driving the individual distributions, or to assess the proportions of data explained, or to measure the connections between specific faunas, habitats and distributions. When faunas are reconstructed from this plot, different habitat types group together, so that they provide an additive pattern that is repeated for mammal communities from similar habitat types. It was shown empirically that the separate analyses produced consistent patterns that indicated habitat type, so that taken together the different taxonomic groups produce parallel patterns of habitat distributions.

This approach is still not taxon-free as it is necessary to analyse each taxonomic group separately, but it does allow for all species to be considered in the same way, using the same measurements, whether living or fossil. It also allows for the modern comparative data set to be
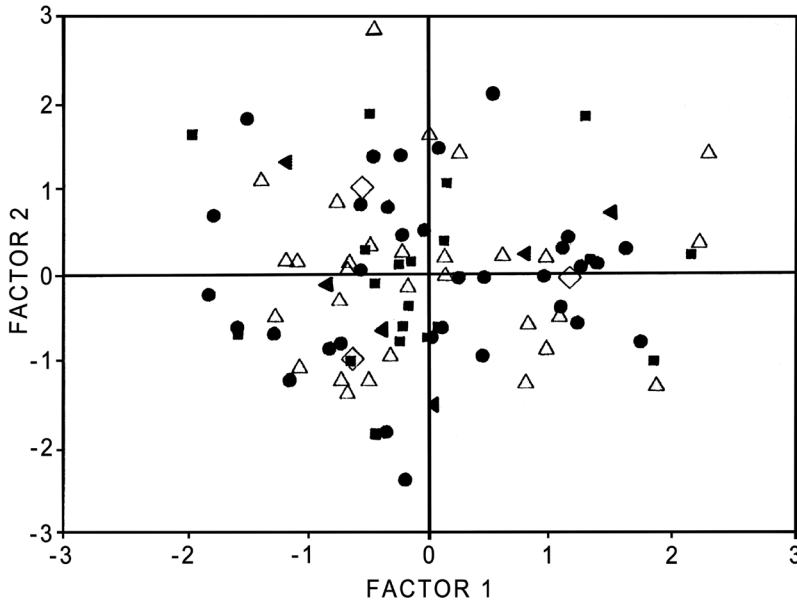
**Fig. 4.** The combined two-dimensional, morphological space occupied by 89 species in the 23 faunas examined. This plot was formed by combining the first two (and most explanatory) factor scores for individual PCAs performed on the five taxonomic groups listed on the figure. Individual plots for each fauna were distinctive for habitat type. Taxonomic groups now overlap and the entire space occupied represents the morphological space for those taxa. When centroids were calculated and plotted for bovids, carnivores and primates, the resultant triangles formed were diagnostic of habitat type. Note: Perissodactyla and Carnivora are now represented with open symbols so that their distribution can be easily seen. ◇ Perissodactyla, ■ Primates, ◀ non-bovid Artiodactyla, △ Carnivora, ● Bovidae.

reduced (in terms of the number of indices used in PCA) to a level that is comparable to fossil assemblages.

Ultimately, in community analyses, even when using the same set of variables for all species considered, the best discrimination of habitat requires that a taxonomic approach be taken to consider each group. The total community information has to be brought together using an additive method, even when limited to postcranial measurements. There are advantages to assessing individual species using the same criteria. Fossil postcrania are often identified to family level only and this study demonstrates that a method of community analysis that relies on postcranial measurements alone can give good results. Classification of fossil material to "large bovid" or "small viverrid" may be sufficient to permit its use. Analyses of this type can be run on collections of postcrania regardless of the ability to assign the material to species to genus. But even at this level, the method is not "taxon-free".

One further consideration is the extent to which samples of fossil assemblages are comparable with living communities (which themselves are always represented by samples). Fossil assemblages can generally be considered to be point accumulations, that is, the animals or plants making up the assemblages are all together in one place. They may not have all lived in one place, for many assemblages can be shown to have originated in two or more different localities, and it is the job of taphonomy to distinguish their sources. For comparison with recent faunas, they too must be point collections (Andrews *et al.* 1979). Saarinen *et al.* (2010) addressed this problem in part by comparing regional fossil mammal faunas in 50 × 50 km grid cells with single fossil faunas present in the grid cells. It was found that the single fossil sites contained about 60% of the fossil species in the grid cells, and that community structure could be estimated accurately from this. In other words, the regional fauna provides a good approximation of the community structure of the mammal fauna. This
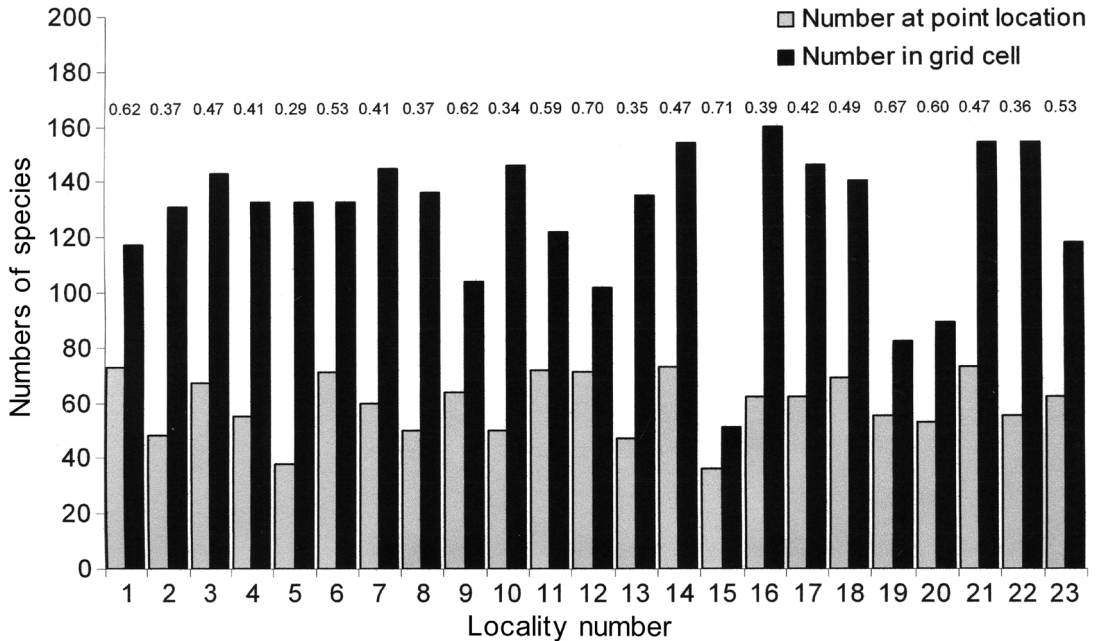
**Fig. 5.** Numbers of mammal species for 23 mammalian faunas. Numbers of species within grid cells (cells 158 km², 25 000 km²) are compared with the 23 locations (collecting localities) falling within the grid cells: 13 of the collecting localities are from single point/time collections (numbers 1, 2, 3, 4, 5, 6, 9, 10, 12, 14, 16, 17, 23) and 10 are regional collections, for example faunal lists for National Parks (numbers 7, 8, 11, 13, 15, 18, 19, 20, 21, 22) within each of the grid cells. The proportions of faunal collections to grid-cell data are shown above the bars. The 23 collecting localities are listed in Andrews *et al.* (1979: table 2), and the grid cell data are from Andrews and O'Brien (2010).

analysis was performed on fossil faunas, however, where there was no independent information on what the community structure actually would have been in the absence of species loss. This approach was tested by comparing regional distributions on a 158 × 158 km grid (Andrews & O'Brien 2010) with the species richness of 13 modern faunas from point localities present within the grid cells (data from Andrews *et al.* 1979). The point localities contain from 29% to 70% of the species present in the regional faunas (Fig. 5), but the three lowest values came from limited-area habitats such as flood plains or local edaphic grassland, and when these are excluded the range of values is 47%–70%. The 10 regional collecting localities analysed by Andrews *et al.* (1979) had 35% to 71% of the species present in the grid cells, with the highest proportions coming from highly uniform habitats. Since the reconstructed habitats can be compared directly with the known habitats, it is possible to say with confidence that even the most poorly represented

point assemblage is still large enough to provide a good estimate of the community structure of the fauna. The opposite is not necessarily true, however, for the locality with the lowest number of species compared with the regional fauna, that for the Serengeti short grass plains, differs from the regional fauna because it is a local fauna (on a regional scale) that is atypical of the region as a whole. The same would be true of any point assemblage that is sampling a local habitat differing from the regional ecology.

## Conclusions

The general conclusion must be that no single method of palaeoecological analysis is entirely taxon-free. The only direct evidence on the ecology of any extinct animal independent of its taxonomy is the isotope signal preserved in its teeth, although this is limited to what it was eating during the time of formation of its teeth.

The other methods considered here all depend at some level on evidence of taxonomy.

- Species richness patterns are based on distinctions between species, but they do not readily distinguish between faunal assemblages from different habitats.
- Size distributions of faunal assemblages are based on size regressions within higher taxonomic groups.
- Ecomorphology targets specific taxonomic groups, but within the group it is partly independent of taxonomy.
- Community ecology describes mammalian communities by their levels of diversity within distinct ecological categories, but these are determined by qualitative (ecological diversity) or quantitative (ecomorphology) methods within taxonomic groups.
- Community ecomorphology combines ecomorphological data for whole communities. It has been found that combining trophic data (dental and/or isotopic) with space use (postcranial data) by multivariate analysis can produce conflicting results, and these sources of evidence are best analysed separately or additively.

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