

Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages

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Abstract.—Evolutionary paleoecology is the study of paleoecological patterns of organization over time. However, identification of such patterns within modern communities must be made before any study over time can be attempted. This research analyzes mammalian ecological diversity of 31 African localities classified into eight vegetation types: forests, closed woodlands, closed woodland/bushland transition, bushlands, open woodlands, shrublands, grasslands, and deserts. Ecological diversity is measured as the relative proportions of large mammal trophic and locomotor behaviors within communities. Trophic and locomotor adaptations are assigned on the basis of published observations and stomach contents of 184 African mammal species. Communities are accordingly described on the basis of total percentages of mammalian trophic and locomotor adaptations. Since many paleoecology studies have been made using taxonomic uniformitarianism, this study also examines taxonomic community structure to compare with ecologically derived patterns.

Results indicate that particular types of vegetation have predictable percentages of arboreal, aquatic, frugivorous, grazing, etc. large mammals. Therefore, these adaptations, because they are predictable in extant assemblages, can be used to predict paleovegetation as well as to portray the community structure of fossil assemblages. Taxonomic groupings also can be used to predict vegetation in extant assemblages, and taxonomic patterns in communities are compared with ecological ones.

The mammalian communities of the Pliocene fossil locality Makapansgat, South Africa, are interpreted using these ecological and taxonomic methodologies. Trophic and locomotor adaptations are assigned for Makapansgat fossil mammals through morphological examination of each taxon. Vegetation type is predicted for these fossil localities, but ecological and taxonomic differences in the assemblages differ from extant communities.

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Accepted: 15 January 1998

Introduction

Cain (1944) described paleoecology as “the study of past biota on a basis of ecological concepts and methods insofar as they can be applied.” More recently, Wing et al. (1992) have defined “evolutionary paleoecology” as the study of paleoecological patterns of organization over time to “bridge the gap between ecology and evolutionary biology.” To examine ecological patterning of past groups of organisms, actualistic studies of modern biotas are necessary so that accurate comparisons with paleofaunas, paleofloras, paleocommunities, and paleoenvironments can be made. Just as functional morphologists apply the comparative method to derive behavior for fossil fauna, known patterns in extant communities can be used to derive information

about the associations of species and their various adaptations over time.

It has long been known that vegetation is determined by abiotic factors such as soil type, light, temperature, rainfall, and evaporation (Coe et al. 1976; Pratt and Gwynne 1977; Kingdon 1977a; Archibold 1995). This study first assesses the dependence of adaptations of large African mammals on vegetation type. Then patterns of association derived from individual ecological adaptations of these mammals are compared with patterns of taxonomic identities in each vegetation type. If ecological or taxonomic patterns exist, they can be used to reconstruct vegetation types for fossil localities, and to examine changes in ecological patterns over time and across geographic regions.

Consideration of Confounding Factors and Paleoeological Methods

There are many factors involved in reconstruction of paleoenvironments and paleoecological structure, such as taphonomy, chronology, and biogeography. Many potential problems can be overcome with selection of appropriate methodology to minimize confounding factors. Several methods of analysis have been consistently used to examine fossil assemblages and to determine the type of vegetation, i.e., forests, woodlands, etc., from which the paleofauna derived. These methods include taxonomic uniformitarianism, functional and ecological morphology (ecomorphology), and ecological diversity.

The taxonomic uniformitarian or taxonomic analogy approach has been used most frequently in the reconstruction of environments (Dodd and Stanton 1990). Using this method, a fossil taxon is compared with its closest living relative to predict ecological behaviors. For example, a fossil bovid is phylogenetically placed in an extant tribe; ranges of ecological parameters, such as preference for wetlands, are outlined for that particular tribe and these ranges are then suggested to be similar for the fossil taxon. Thus, on the basis of phylogeny the autecology of the taxon is defined as well as the environment in which the taxon existed. This approach can be quite accurate for reconstructing past environments. However, problems include a lack of morphological analysis of the fossils, and an ecological bias that may result from the use of only one taxon or taxonomic group (Cooke 1978). Other problems include ecological preferences in higher taxonomic groups changing over time, and human-induced reduction of habitat altering ranges for many species. Taxonomic analogy may not be the ideal method to use for ecological reconstructions, but for this study, the taxonomic composition of mammal communities will be compared with the ecological composition to examine this methodology further.

Functional morphology and the comparative method usually entail morphological analyses to arrive at the ecological behavior of a particular taxon or taxonomic group using

extant taxa as a basis for comparison to fossil animals. This is the best way to determine adaptations of particular animals in the fossil record. However, this is not a good methodological approach for understanding paleocommunities unless all taxa are studied. Ecological morphology or ecomorphology has traditionally been the morphological examination and subsequent multivariate analysis of adaptations within particular lineages (e.g., Kappelman et al. 1997). Morphological analysis is directly related to environmental parameters such that animals preferring forests are classified together, animals preferring grasslands are classified together, etc. In this way, the likely vegetation for fossil animals can be determined. Again, this usually entails the use of only one group of animals.

Ecological diversity analysis has been used to create environmental profiles (or spectra) by assigning taxonomic, trophic, locomotor, and body size attributes to mammalian members of extant communities (Fleming 1973; Andrews et al. 1979), and paleocommunities (Andrews et al. 1979; Van Couvering 1980; Artemiou 1983; Andrews 1989). Ecological spectra are actually histograms of percentages of ecological attributes that are compared with one another and tested with contingency tables for significant differences between spectra. Modern communities have been compared with fossil assemblages to establish probable vegetation types (Andrews et al. 1979; Nesbitt-Evans et al. 1981; Artemiou 1983; Andrews 1989). This methodology is important because it uses mammalian adaptations to predict vegetation, without being concerned with mammalian taxonomy. The transformation of taxa into ecological characteristics and their subsequent analysis is suggested to be phylogeny-free because these data become separated from both the specific taxa and their historical circumstances (Damuth 1992). The results derived from this phylogeny-free information transform faunal assemblages into ecological communities that can be compared with any other community throughout time as the parameters used to construct the paleovegetation are not taxon specific (Andrews et al. 1979). Nevertheless, previous applications of this method have not

included functional morphological analyses of each fossil taxon in an assemblage, but many trophic and locomotor parameters were assigned through qualitative morphological and taxonomic analogy. When functional morphological analyses are used, predicted ecological adaptations for each taxon should be more accurate and thus the resultant ecological diversity analyses represent community structure more dependably. Taphonomic problems with the abundance of taxa, caused by various processes, are reduced because only presence/absence data are used. Fossil localities are also more easily compared with either modern data or other fossil localities because taxonomic differences due to temporal or geographic separation are eliminated.

I have termed ecological diversity "phylogeny-free" rather than "taxon-free" (Damuth 1992) because each taxon must be identified, if only on morphological terms, so that trophic and locomotor behavior can be analyzed. What the taxon is called is irrelevant. However, are fossil species removed from their historical circumstances using this method? Ecological diversity analysis attempts to determine if the ecological adaptations of some communities are the same as, similar to, or not the same as those of other communities, irrespective of the taxonomic composition. Technically, an African antelope could be compared with an Australian kangaroo if each was considered a terrestrial grazer. However, there are mammals filling niches in African vegetation because they have evolved there, and this history could affect the outcome of the ecological pattern in communities. In the case of the African Plio-Pleistocene, the taxonomic composition includes the same orders represented in extant communities. Thus, taxonomic representation is similar, although some families from the Plio-Pleistocene are now extinct and there have been shifts in the numbers of species present in tribes. It therefore seems reasonable to assume that as the historical circumstances are similar in extant and extinct African communities, ecological comparisons between them are possible. As evolutionary history is somewhat constrained, possibly even locally, each geographic region and time period should have its own compar-

ative sample dependent upon the questions asked (Andrews 1996). However, the importance of using ecological diversity is to eventually compare assemblages over larger geographic space and subsequently longer time spans to assess patterns of ecology and evolution.

Extant African Vegetation

African vegetation has previously been categorized into general vegetation types such as forest, woodland, grassland, etc. (Lind and Morrison 1974; Pratt and Gwynne 1977; White 1983). Because the purpose of this study is to provide comparative material for fossil assemblages, I used these broad vegetation types. For example, forest includes rain, temperate, and montane forests. Fossil assemblages are more likely to represent these broadly defined types rather than specific vegetation, such as secondary or disturbed forests, because of possible time and space averaging of animals in fossil assemblages. In general, classifications of extant environments grade from areas of high annual rainfall (forests) to those that are extremely dry (deserts). Between these two extremes, the vegetation structure decreases in density of trees and other woody vegetation as rainfall decreases. However, features of the landscape and the impact of fires, herbivores, and humans influence plant life in extant communities so that this gradient is not direct (Bourlière and Hadley 1983). Consequently, vegetation categories used in this study are broad enough to be discerned in the fossil record, but specific enough that the mammalian adaptations and taxonomic groups are predictable within them. I collected published data about extant African localities including mammalian fauna, vegetation, and abiotic information. Localities reported to be greatly altered by humans were not included, such as the "derived savanna zone" in central Nigeria (Happold 1987).

Forests

Almost all forests in Africa are evergreen or semi-evergreen. They consist of three major types: lowland rain, montane, and dry or seasonal forests. A rain or lowland forest is typified by tall, columnar trees from 10 to 60 me-

ters in height, with a multi-structured canopy (Lind and Morrison 1974; Pratt and Gwynne 1977). The forest usually contains a shrub layer, although ground vegetation is commonly sparse or even absent. Rain forests in different African geographic zones possess different species of trees and other plants in high diversity, although the overall structure is similar. Average annual rainfall is greater than 1600 mm per year in these forests. Montane forests (those above 2000 m) consist of deciduous and evergreen trees at lower altitudes, bamboo forests at mid-altitudes, and forests with shorter trees (12 to 18 m) at the highest elevations (Lind and Morrison 1974). Rainfall in montane forests is usually greater than 1100 mm per annum. Dry (seasonal tropical) or temperate forests have lower plant species diversity than lowland forests and usually have pronounced dry seasons with low humidity. Seasonal forest trees are usually fairly short, with a single, closed canopy level (White 1983); there is dense underbrush, and ferns are prevalent (Lind and Morrison 1974). Mean annual rainfall in these semi-deciduous forests ranges from 875 mm to 1000 mm annually.

Savannas

Many Pliocene paleoecological reconstructions use "savanna" or "savanna-woodland" to encompass vegetation that is intermediate between forests and deserts. However, the term savanna was originally used to describe treeless regions in South America (Archibold 1995). Bourlière and Hadley (1983) note three keys to identifying a savanna: (1) a continuous grass layer, important to the biozone, is interspersed with trees or shrubs; (2) bush fires occur occasionally; and (3) the regions have distinct wet and dry seasons that control the growth of the vegetation. With reference to the second and third elements, structure of the savanna changes depending on frequency of burning and severity of dry seasons, such that as aridity increases the vegetation structure of the savanna becomes less complex. Because of this alteration in plant content and structure, the term savanna reflects a process rather than a category. Thus, several vegetation types fall under the umbrella term "savanna." For this

reason, I prefer to use the terms woodland, shrubland or scrub woodland, and grassland for vegetation classifications, and use savanna only as a process of growth.

Woodland.—This is the most widespread vegetation category in Africa today. Woodlands consist of trees that are branched (Lind and Morrison 1974), deciduous, and range from 8 to 20 m in height. Trees in woodlands contribute more than 20% (Pratt and Gwynne 1977) or 40% (White 1983) of the vegetation cover. Coverage is based on crown diameters such that from an aerial view the surface area is covered by the crowns of trees in various percentages (Pratt and Gwynne 1977). The canopy can be relatively continuous, but crowns are not interlaced or complex (Lind and Morrison 1974). Using average tree coverage, I subdivided woodlands into three groups: open woodlands, approximately 20–25% tree coverage; medium density woodlands with about 30–45% tree cover; and closed woodlands, with 50% or greater tree coverage. Ground cover in all woodlands consists of herbs and grasses. The mean annual rainfall in woodlands ranges from 600 mm to 1100 mm with greater amounts of rainfall coinciding with heavier tree cover.

Scrub woodlands generally occur in areas with low rainfall and poor soil regimes. These woodlands have tree species that are no more than three meters tall, although they are typical African, woodland tree species, e.g., *Acacia*. In this study they have therefore been classified as shrubland.

Shrubland.—Vegetation dominated by shrubs, e.g., plants that vary from 10 cm to 2 m or more in height, is called shrubland. These plants contribute more than 20% of the land cover. Taller trees contribute less than 10% of the total vegetation; poor quality (i.e., low crude protein content) grasses and small dicots make up the rest of the ground cover (Pratt and Gwynne 1977). Taller woody plants do not grow because of low rainfall, seasonal drought, and low temperatures. Annual rainfall ranges from 400 mm to 650 mm and is highly seasonal, with no rain falling for approximately six contiguous months.

Grassland.—Two basic grassland types are recognized in Africa: secondary/derived and

edaphic. Secondary or derived grasslands are often called open or grassland savannas (Lind and Morrison 1974). These grasslands are created by regular burning and/or grazing pressure. Without these pressures, the vegetation could return to bushland, woodland, or even forest (White 1983). Derived grasslands are dominated by grasses and herbs, with widely scattered groups of trees and shrubs. Trees or bushes do not exceed 2% of the ground cover (Pratt and Gwynne 1977). Mean annual rainfall ranges from 400 mm to 700 mm with a long dry season and a rainy season of three or four months.

Edaphic grasslands are associated with seasonally or permanently waterlogged soils, also called wetlands, flats, or vleis (White 1983). The plants associated with these regions are aquatic grasses and sedges. When these plants spread into shallow lakes, they become swamps. Swamps can also form along rivers in valleys, with *Papyrus* being the dominant plant form (Lind and Morrison 1974). Meandering river systems also produce floodplains and deltas that support edaphic grasslands.

Bushland

Bushes constitute 40% or more of the ground cover in this vegetation type. A bush is a woody plant intermediate between a shrub and a tree, usually 3–7 m in height, with multiple main branches that are at least 10 cm in diameter (White 1983). Trees also exist in bushlands, and although some grass grows in these regions, they are not “savannas” because the grass is not important to the biozone (White 1983). Bushland occurs where 250 to 500 mm of rainfall per year occurs seasonally.

Desert

Desert vegetation occurs in regions of low rainfall and high evapotranspiration rates throughout most of the year. Many succulent plants occur in these regions, which in Africa include the Sahara and Namib Fog Deserts.

Extant Community Methods

I first compiled lists of large mammalian species from 31 localities in sub-Saharan African national parks, game reserves, and spe-

cifically defined vegetation zones (Swynnerton 1958; Lamprey 1962; Child 1964; Vesey-Fitzgerald 1964; Sheppe and Osborne 1971; Smithers 1971; Lind and Morrison 1976; Ansell 1978; Rautenbach 1978a,b; Behrensmeyer et al. 1979; Perera 1982; Bremen and de Wit 1983; Emmons et al. 1983; White 1983; Lanjouw 1987; Happold 1987; Skinner and Smithers 1990). While regions severely altered by human intervention were excluded, most African habitats have been somewhat altered by humans and this should be considered for paleoenvironmental reconstructions. Data on rainfall, tree cover, temperature, and seasonality were also collected. These 31 localities were each assigned a vegetation category (see Appendix 1). Several localities included mosaic vegetation. In these cases, localities were classified by overall dominant vegetation types. For example, the Okavango Delta, while known for wetlands, is surrounded by shrubland/scrub woodland vegetation, and thus is classified as shrubland. Several localities were intermediate between vegetation categories. These included closed woodland/bushland transition (Natal Woodland and West Lunga NP) and shrubland/grassland transition (Sahel Savanna). Two national parks were subdivided into different vegetation classifications because mammal lists were available for specific vegetation types. Serengeti National Park was included as (1) the complete park and therefore a mosaic dominated by bushland, (2) bushland-only regions of the park, and (3) open grassland, the Serengeti Plains. Kafue National Park encompassed (1) woodland and edaphic grassland and (2) edaphic grassland only.

After preliminary investigations using both micro- and macromammals, I restricted the analysis to non-volant macromammals (Reed 1996). First, many micromammals are geographically restricted, and for taxonomic analyses, biogeography confounded ecology. Second, at many Plio-Pleistocene fossil sites, micromammals (Orders Chiroptera, Rodentia, Insectivora) are often poorly represented and accumulated separately from macromammals. Therefore I included only larger mammals, usually those above 500 grams. If a family or tribe possessed animals both above and

TABLE 1. Definitions of mammalian adaptations.

Ecological category	Defining characteristic	Example
Trophic category		
Carnivore	Eats meat	<i>Panthera leo</i> (lion)
	Eats meat/bone	<i>Crocuta crocuta</i> (hyena)
	Eats meat/invertebrates	<i>Mungos mungo</i> (mongoose)
Insectivore	Eats insects/invertebrates	<i>Manis tricuspis</i> (pangolin)
Herbivore	Eats grass (grazer)	<i>Connochaetes taurinus</i> (wildebeest)
	Eats edaphic grasses (fresh-grass grazer)	<i>Kobus kob</i> (kob)
	Eats leaves (browser)	<i>Tragelaphus strepsiceros</i> (kudu)
	Eats grass and leaves (mixed feeder)	<i>Aepyceros melampus</i> (impala)
	Eats roots/bulbs	<i>Hystrix africaeaustralis</i> (porcupine)
Frugivore	Eats fruit/leaves/insects in various combinations	<i>Papio ursinus</i> (Chacma baboon)
Omnivore	Three or more of the above with no preference	<i>Melivora capensis</i> (honey badger)
Locomotor category		
Arboreal	Moves and feeds in trees most of the time	<i>Galago moholi</i> (bushbaby)
Aquatic	Feeds or locomotes in water 50% of the time	<i>Hippopotamus amphibius</i> (hippo)
Fossorial	Lives or acquires food underground by digging	<i>Orycteropus afer</i> (aardvark)
Terrestrial	Moves and feeds on the ground	<i>Equus burchelli</i> (zebra)
Terrestrial/arboreal	Moves and feeds on the ground and in trees	<i>Panthera pardus</i> (leopard)

below that weight, the entire family was included.

Mammals were assigned locomotor and trophic adaptations (Table 1) based on published behavioral observations and analysis of stomach contents (Dorst and Dandelot 1969; Kruuk 1972; Kingdon 1974a,b, 1977, 1979, 1982a,b; Smithers 1971; Hoffman and Stewart 1972; Delaney and Happold 1979; Happold 1987; Skinner and Smithers 1990; Estes 1991; Kitchner 1991). There were 184 large mammal species from all localities (Appendix 2).

After species were assigned to trophic and locomotor categories, the percentage of species in each category was calculated for each community (Appendix 1). The percentages of each adaptation, e.g., percentage of arboreal locomotion, were analyzed by vegetation type using a Kruskal-Wallis test for differences in single classification ranked data. These categories were further analyzed with Mann-Whitney *U*-tests for differences between two samples of ranked observations.

While particular species or genera are likely associated with vegetation types, analyses could not be completed on such small sample sizes. In addition, species and genera are not necessarily shared among the same vegetation types in distant geographic provinces; thus tribes and subfamilies were the most logical taxonomic groups to use for analysis. How-

ever, if an order or family consisted of only one or two species, these higher taxonomic groupings were used.

Discriminant function analyses (DFA) were used as a classification technique to see (1) how reliable adaptations and taxonomic groupings were for assigning each community to a specific vegetation type and (2) to eventually assign fossil assemblages to a vegetation type with probabilities of accurateness. DFA had the added advantage of using all ecological adaptations or taxonomic groupings in the analyses.

Results of the Extant Community Study

Comparisons of Adaptations and Vegetation

Locomotor and Trophic Adaptations.—I performed a Kruskal-Wallis test on locomotor and trophic percentages from each vegetation category. The desert category was omitted because of the sample size of one. The Kruskal-Wallis test showed significant differences between all vegetation groups at $p < 0.001$ for the adaptations listed in Table 2. However, to analyze pairs of vegetation categories more rigorously, I tested differences between communities with the Mann-Whitney *U*-test. This test showed significant differences between some pairs of communities at $p < 0.05$ (Table 2). Because the closed woodlands and closed

TABLE 2. Mean and range of significant adaptations for each vegetation type.

	A	C	CB	F	G	I	OM	R	T	TC	TF
Forests <i>n</i> = 7	Mean SD Range	0.308 0.051 0.140	0.107 0.028 0.088	0.000 0.000 0.000	0.074 0.044 0.118	0.000 0.000 0.000	0.041 0.045 0.121	0.103 0.021 0.052	0.365 0.125 0.357	0.156 0.089 0.232	0.439 0.063 0.197
Closed Wood Transition <i>n</i> = 4	Mean SD Range	0.107 0.039 0.082	0.148 0.030 0.069	0.038 0.003 0.005	0.099 0.016 0.039	0.071+ 0.030 0.059	0.037 0.013 0.031	0.065 0.010 0.022	0.540 0.068 0.157	0.330 0.016 0.036	0.225+ 0.035 0.078
Bushlands <i>n</i> = 4	Mean SD Range	0.058 0.004 0.009	0.123 0.009 0.020	0.040 0.013 0.032	0.100 0.034 0.083	0.098*+ 0.017 0.039	0.033 0.028 0.067	0.063 0.029 0.071	0.014 0.011 0.025	0.295 0.012 0.027	0.192+ 0.026 0.057
Open Wood <i>n</i> = 5	Mean SD Range	0.040 0.011 0.026	0.159 0.046 0.101	0.042 0.012 0.030	0.112 0.047 0.117	0.131* 0.040 0.093	0.040 0.024 0.060	0.053 0.022 0.050	0.013 0.008 0.020	0.335 0.042 0.106	0.124 0.008 0.018
Shrubland <i>n</i> = 7	Mean SD Range	0.014 0.009 0.022	0.161 0.045 0.133	0.047 0.013 0.034	0.194 0.062 0.181	0.148 0.051 0.169	0.100 0.046 0.135	0.053 0.034 0.097	0.591 0.057 0.171	0.316 0.058 0.180	0.076 0.009 0.022
Grassland <i>n</i> = 3	Mean SD Range Variance	0.000 0.000 0.000 0.000	0.173 0.037 0.070 0.001	0.087 0.062 0.109 0.004	0.119 0.080 0.144 0.006	0.223 0.054 0.101 0.003	0.068 0.059 0.105 0.003	0.053 0.053 0.105 0.003	0.701 0.130 0.257 0.017	0.353 0.033 0.063 0.001	0.034 0.030 0.054 0.001
Kruskal-Wallis <i>df</i> = 5, <i>p</i> =	27.675 0.000	12.663 0.027	18.583 0.002	17.726 0.003	23.353 0.000	11.220 0.047	11.434 0.043	16.299 0.006	15.056 0.010	16.341 0.006	27.748 0.000

Kruskal-Wallis showed significant differences between groups for all vegetation types at $\chi^2_{0.05}$. Mann-Whitney *U*-tests between each pair of communities showed significant differences at *p* < 0.05 for arboreal and terrestrial locomotion, and for grazing and total frugivory except as indicated below.

* No significant difference between bushland/open woodland.

+ No significant difference between closed woodland/bushlands.

Abbreviations: A = arboreal; C = meat; CB = meat/bone; F = fossorial; G = grass; I = insects; OM = omnivorous; R = roots/bulbs; T = terrestrial; TC (total carnivory) = meat, meat/invertebrates, meat/bone; TF (total frugivory) = fruit, fruit/insects, fruit/leaves.

woodland/bushland transition regions each had an $n = 2$, they were grouped together for the Mann-Whitney U -tests.

The percentage of mammals exhibiting arboreal locomotion in each vegetation category reflected tree cover and amount of rainfall. Forests have the greatest percentages of mammals with adaptations to arboreality. These arboreal mammals include members from the orders Primates, Carnivora, Hyracoidea, and Pholidota. In the remaining vegetation categories, percentages of arboreality decrease as tree cover and rainfall decrease (Appendix 1). Tree cover is partially a result of rainfall; that is, in areas of high rainfall there are usually more trees than in areas with low or strikingly seasonal rainfall.

I performed a regression analysis of arboreal locomotion percentages against mean annual rainfall in these localities. There was a significant correlation ($p \ll 0.001$) between these variables (percentage of arboreal locomotion = $0.275 * (\text{rainfall in cm}) - 0.135$), and the rainfall regime accounted for 83% ($r^2 = 0.827$) of the variation seen in the percentage of arboreal mammals among vegetation types. This correlation between rainfall and arboreal locomotion is the result of greater amounts of rainfall providing more vegetation levels, thus contributing more structural diversity for arboreal locomotor adaptations.

High percentages of aquatic locomotion in communities obviously identified areas with rivers and lakes, as well as floodplains and deltas. Because all vegetation categories included some localities in which there are rivers, floodplains, etc., a statistical test to show differences between localities was not useful for this adaptation. Aquatic mammals included species from the groups Hippopotamidae, Mustelidae, Rodentia, Tragelaphini, and Insectivora.

The percentage of fossorial mammals did not significantly separate vegetation types, although in open dry regions there tended to be higher percentages of these mammals. Percentages of terrestrial/arboreal locomotion were also not significantly different among vegetation types. Because this adaptation indicates animals, such as leopards and baboons, that use trees if they are available, the

lack of correlation of this behavior to tree density is to be expected. Finally, for percentages of terrestrial locomotion, differences among vegetation categories were statistically significant for those vegetation categories noted in Table 2.

Several trophic adaptations were also statistically significant when examining differences among communities, and those associated with frugivory followed a tree cover/rainfall gradient similar to that of arboreal locomotion. Percentages of frugivorous, meat-eating, meat/bone eating, and grazing mammals separated forests from all other vegetation categories. In addition, these trophic adaptations were statistically significant between several other pairs of vegetation types (Table 2).

In general, high percentages of frugivorous mammals indicated vegetation categories with greater tree or bush cover and rainfall. Specifically, percentages of frugivorous mammals separated bushlands from medium and open density woodlands. These bushlands contain higher percentages of frugivores ($\geq 17\%$) than sparser woodlands although they both possess roughly the same percentages of arboreal animals (Table 2, Appendix 1). Sept (1994) has shown that there are more plant genera bearing edible fruit in bushlands than in woodlands; thus, greater percentages of mammalian frugivory in bushlands possibly reflect increased genera of plants with edible fruit. Whether this reflects actual production, and therefore abundance of fruit in bushlands, needs to be examined. Frugivorous mammals include some primates and bovids.

None of the forests used in this study were inhabited by meat/bone eaters (hyaenids), but this adaptation has been reported in some tropical seasonal forests (Andrews et al. 1979). In general, the more arid a region, the more meat/bone eating mammals it contains, although there are only a maximum of three extant African mammals that consume bones in any one region. The Serengeti Plains contains all three of these mammals (*Lycaon pictus*, *Hyaena hyaena*, and *Crocuta crocuta*), while having a very small total community of large mammals (19). Consequently, the percentage of animals having adaptations to meat/bone eating is almost 16% on these plains (Appendix 1).

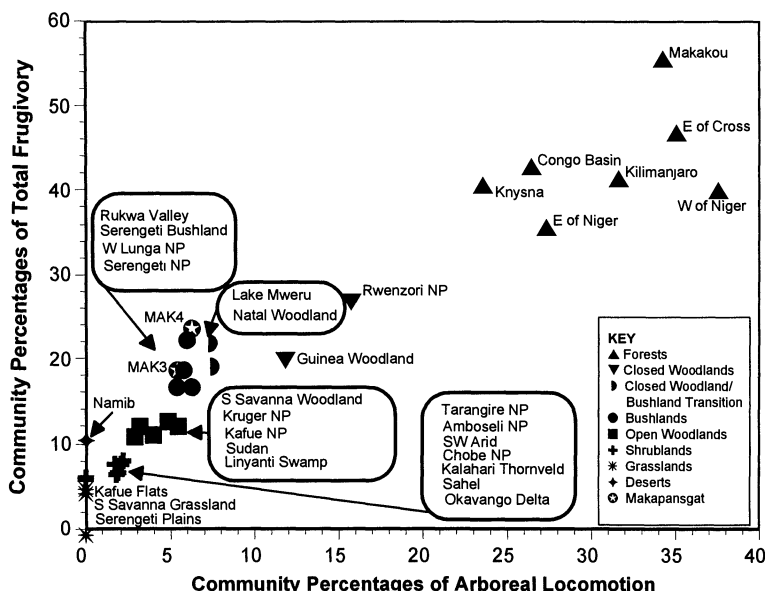


FIGURE 1. Percentages of arboreal locomotion vs. percentages of frugivory in African vegetation types. The percentages of these two adaptations in mammalian communities separates the open, drier habitats from closed, mesic ones. Forests are above 20% arboreal locomotion and 30% frugivory. Fossil localities are positioned with bushlands (Makapansgat Member 3) and closed woodland/bushland transition (Makapansgat Member 4).

Closed woodlands have fewer grazers than woodlands and grasslands that are more open (Table 2). Grazing separates plains from shrubland regions because shrublands usually have poorer types of soil and low rainfall (Breman and de Wit 1983). For example, the Sahel Savanna (Nigeria), although producing short-season grasses for about three months, is a shrubland throughout the year. Therefore, the Sahel has relatively few grazing animals. Grazing mammals include representatives from the families Bovidae (Alcelaphini, Hippotragini, Reduncini), Suidae, Equidae, Rhinocerotidae, plus the orders Rodentia and Lagomorpha. There are no strictly grazing mammals in forests.

Fresh-grass grazers are abundant in communities where there are edaphic grasslands, in floodplains, and in lake margins such as Kafue Flats, Sahel Savanna, Okavango Delta, Lake Mweru, Chobe National Park, Linyanti Swamp, and Kafue National Park. In addition to some members of the bovid tribe Reduncini, other fresh-grass grazers include members from the Hippopotamidae and Thryonomidae (Rodentia). The number of fresh-grass grazers fluctuates within vegetation type. The Oka-

vango Delta, for example, has a high proportion of fresh-grass grazers compared with other shrublands and the Linyanti Swamp has a high percentage in comparison to other open woodland regions.

Other trophic adaptations, including browsing, meat eating, meat/insect eating, mixed-feeding, omnivory, insectivory, and root and bulb feeding, were not statistically significant among pairs of vegetation types. Therefore these adaptations are not useful for predicting vegetation types in fossil assemblages. However, while these adaptations do not differentiate vegetation on a univariate level, they are important for examining patterns in community structure.

I examined adaptations that were significantly different among vegetation types in bivariate plots to show graphically how these community adaptations separated vegetation types (Figs. 1, 2). While several of the taxonomic groups are identified with particular vegetation types (e.g., primates with forests), they are not as discriminating as adaptations (e.g., arboreal mammals with forests). Thus, plotting taxonomic groups against one another

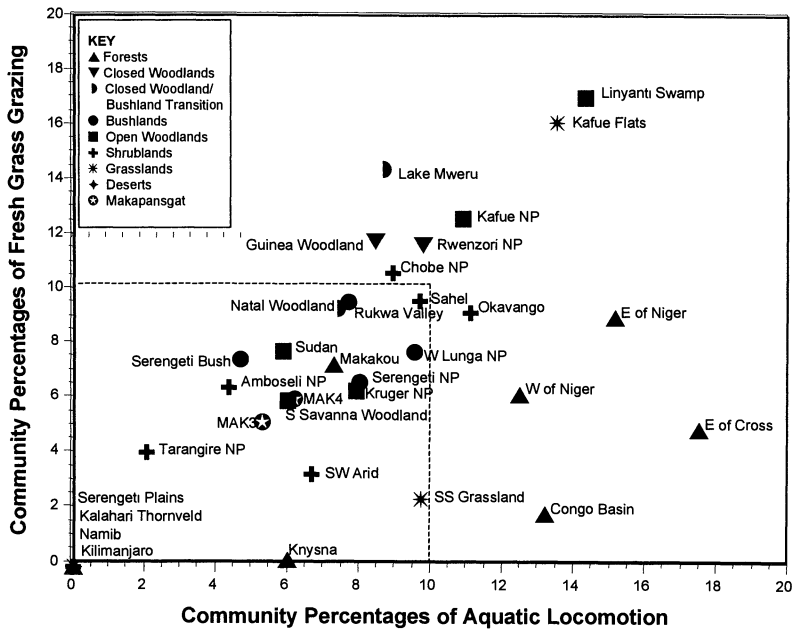


FIGURE 2. Percentages of aquatic locomotion vs. percentages of fresh-grass grazing. These two adaptations separate vegetation types with edaphic grasslands, floodplains, swamps, and wetlands from the other vegetation. Localities outside of the dotted line at 10% are those with abundant edaphic grasslands, wetlands, or swamps. The fossil localities are grouped with the vegetation types within the box.

er was not useful for separating vegetation types.

Discriminant Function Analyses

Discriminant Function Analysis (DFA) was conducted to assess the ability of either taxonomic groupings or mammalian adaptations to correctly classify extant and, in turn, fossil vegetation types. The first DFA used percentages of taxonomic groupings in each vegetation type and the second DFA used percentages of ecological adaptations in each vegetation type. The analysis was run on raw percentages and on arcsine transformations (Sokol and Rohlf 1981) with no major differences in results. Each extant locality was assigned to a category based on its vegetation type (Appendix 1). As there was only one desert, this was left out of the analysis because discriminant function requires at least two members in a classification. A stepwise DFA was performed using Mahalanobis distance (D^2) with the Statistical Package for the Social Sciences (SPSS Inc. 1996). This method produced the largest D^2 between the two closest vegetation types at each step. An F-ratio with

a minimum of 1 was used to enter a variable (either taxonomic or adaptation group) into the analysis.

Taxonomic.—There were 37 different taxonomic groupings (Appendix 3). As DFA requires that a variable have a minimum tolerance level, 14 of these taxonomic groupings were not used in the analysis. These taxonomic groups were detected as being redundant. The first function, based on the remaining 23 groups, accounted for 99.3%, and the second function only 0.5%, of the variation among these taxonomic groups. The first two functions were significant (Table 3) at the $p \ll 0.001$ level. The pooled within-groups correlation table showed that the taxonomic groups Pedetidae and Giraffidae were mostly highly correlated with function 1, while Thryonomidae, Manidae, Tragulidae, and Hippopotamidae were most highly correlated with function 2. The DFA classified 100% of the localities into their vegetation types using the taxonomic groupings. The F-test between groups was significantly different between some pairs of vegetation types, although the more general-

TABLE 3. Discriminant function analysis for vegetation types using taxonomic identities of mammalian communities. Variables ordered by absolute size of correlation within function; abbreviations as in Appendix 3.

(a) Structure matrix (pooled within groups correlations between functions and variables)					
Variable	Function 1	Function 2	Variable	Function 1	Function 2
MAN*	-0.066	-0.304†	MUST	0.007	-0.024
HIPPO*	-0.017	-0.271†	HERP	0.002	0.027
TRAGU*	0.006	-0.233†	HYRA	-0.006	0.051
PONG*	0.035	-0.146†	PAPI	-0.005	0.036
PED*	-0.202	-0.199	LAG	0.006	-0.029
GIR*	-0.135	0.036	THRY*	-0.108	-0.322
BOV*	0.042	-0.175	SUID*	0.020	0.029
AEPY	0.006	0.040	COLO	-0.003	0.055
CEPH	-0.011	0.061	LORIS	-0.015	0.080
TUB	0.006	-0.035	ANTEL	0.004	-0.040
RHINO	0.002	0.003	MUR	-0.009	0.013
NEO	0.005	0.037	ALCE	0.016	0.004
ELEP	-0.003	0.025	HYAEN	0.023	-0.031
CAN*	0.086	-0.038	HYS	-0.006	-0.033
VIV*	0.008	-0.038	TRAG	0.000	0.020
CERC	-0.020	0.092	PEL	0.003	-0.015
HIP*	0.040	0.117	INS	-0.003	0.004
FEL*	-0.107	0.116			
EQU*	0.003	0.060	Eigenvalue	14,082	70
RED	0.009	0.052	% Variance	99.3	0.5
			Significance	$p < 0.001$	$p < 0.001$

(b) F-test between groups (df = 23,2)					
Category	CW	B	OW	S	G
Forests	378.569 $p < 0.003$	466.435 $p < 0.002$	655.146 $p < 0.002$	611.86 $p < 0.002$	826.029 $p < 0.001$
Closed woodland		5.584 $p < 0.163$	17.730 $p < 0.053$	4.767 $p < 0.18$	100.978 $p < 0.010$
Bushland			6.804 $p < 0.136$	5.703 $p < 0.16$	73.034 $p < 0.014$
Open woodland				10.699 $p < 0.089$	45.287 $p < 0.022$
Shrubland					93.765 $p < 0.011$

Abbreviations: CW = closed woodland, B = bushland, OW = open woodland, S = shrubland, G = grassland.

* Variable not used in the analysis.

† Largest absolute correlation between variable and all discriminant functions.

ized vegetation was not significantly different from one another (Table 3).

Ecological Adaptations.—This DFA was conducted using 14 ecological adaptations to classify the localities into vegetation types. The first two functions accounted for 88.2% and 9.5% of the variance among the adaptations. The first two functions were significant at the $p < 0.001$ level. The pooled within-groups correlation table showed that arboreality, frugivory, and grazing are most strongly correlated with function 1, while arboreality, frugivory, and fresh-grass grazing are most strongly correlated with function 2 (Table 4).

This analysis classified 100% of the adaptations of large mammals into the correct veg-

etation types. Despite the accuracy of the classifications, an *F*-test showed significant differences among all vegetation types for steps 4–9 only. The final step (12) showed that three vegetation types were not significantly different from one another (Table 4). This is approximately the same result shown by the Mann-Whitney *U*-tests between some vegetation types.

DF Comparisons.—The discriminant functions classified all of the extant vegetation types correctly using both taxonomic and ecological factors. The significance of this is shown both in the size of the eigenvalues and in Wilk's Lambda tests of each function. However, the taxonomic DF was able to use only

TABLE 4. Discriminant function analysis for vegetation types using ecological adaptations of mammalian communities. Abbreviations as in Appendix 1.

Variable	(a) Structure matrix (pooled within groups correlations between functions and variables)	
	Function 1	Function 2
A	-0.359*	0.150
TF	-0.315*	0.184
R	-0.080	-0.078
F	0.056	-0.041
I	0.032	-0.077
TA	-0.019	0.073
T	0.115	0.039
MF	0.054	0.015
G	0.282	0.027
OM	-0.055	0.017
B	-0.002	0.059
TC	0.114	0.104
FG	0.022	0.138
AQ	-0.018	0.057
Eigenvalue	139.75	13.83
% Variance	89.4	8.8
Significance	$p < 0.001$	$p < 0.002$

Category	(b) F-test between groups (df = 14,11)				
	CW	B	OW	S	G
Forests	29.629 $p < 0.001$	34.677 $p < 0.001$	53.567 $p < 0.001$	83.570 $p < 0.001$	59.672 $p < 0.001$
Closed woodland		1.273 $p < 0.349$	3.339 $p < 0.026$	13.243 $p < 0.001$	14.325 $p < 0.001$
Bushland			1.525 $p < 0.244$	7.634 $p < 0.001$	9.501 $p < 0.001$
Open woodland				4.302 $p < 0.010$	5.922 $p < 0.003$
Shrubland					2.003 $p < 0.126$

Abbreviations: CW = closed woodland, B = bushland, OW = open woodland, S = shrubland, G = grassland.

* Largest absolute correlation between variable and all discriminant functions.

about two-thirds of categories. The discrimination between vegetation types was much larger using taxonomic groupings; that is, the centroids of each vegetation type on each function were much farther apart than when using ecological adaptations. This is likely because some of the rare taxonomic groups were only found in particular vegetation types, e.g., Pongidae and Tragulidae in forests, Peleinae in grasslands, etc. Where there are no rare taxonomic groups, vegetation is harder to reconstruct. However, the absence of a single rare species would not affect the result of a vegetation reconstruction based on percentages of species in each ecological adaptation. In predicting vegetation for fossil localities, it is probably best to compare both types of data if possible for the most accurate reconstruction of vegetation types.

Extant Community Discussion

Large mammal ecological structure, represented by percentages of species exhibiting particular trophic and locomotor adaptations in African communities, is apparently dependent upon vegetation. Several adaptations exist in percentages that can be predicted on the basis of vegetation type. For example, relative proportions of arboreal locomotion are dependent upon the vegetation such that as tree cover declines, percentages of arboreal mammals decline. Percentages of arboreal locomotion can be used successfully to estimate mean annual rainfall in extant communities. In Africa, high annual rainfall is associated with forests and seasonally low annual rainfall is associated with arid shrublands and deserts. There is, consequently, a direct correlation between the amount of rainfall and type of vegetation.

Because percentages of arboreal locomotion are predictable depending on vegetation, it follows that vegetation can be estimated by the percentages of arboreal locomotion, as well as other locomotor and trophic adaptations. The prediction values of some adaptations are better than others, and if the purpose of a study is to reconstruct paleovegetation from a fossil assemblage, it is best to use those adaptations known to differentiate vegetation types. The percentage of mixed feeding, for example, is not associated with changes in vegetation and is therefore unimportant in reconstructing vegetation. Nonetheless, all adaptations are important when comparing community structure among extant and extinct communities.

Discriminant function was successful in identifying vegetation types from both mammalian adaptations and taxonomic groupings. The adaptation analysis also showed what the univariate analysis revealed: arboreality, frugivory, and grazing are highly dependent on vegetation. All of the extant vegetation types were classified correctly, despite the fact that *F*-tests between three vegetation type pairs were not significantly different. This result is likely a function of two factors. First, sites that are not significantly different include more intermediate vegetation types, and as such, are difficult to separate with these more generalized mammalian adaptations. Second, as sample sizes of some vegetation types are low, it is perhaps difficult to get significant results. Adaptations were slightly better than taxonomy at distinguishing between vegetation types, considering the *F*-tests of the DF. However, this could be caused by certain taxonomic groups comprising species from different vegetation types, e.g., Suidae. These tribes and families are comparable to the more generalized adaptations.

These analyses have also shown that mammals with more generalized adaptations exist in all regions, but are prevalent in vegetation that can be considered intermediate. Thus, some African taxonomic groups are more generally widespread, while some are associated with particular vegetation types. For example, many arboreal animals are primates. As vegetation types become more open and arid, the

percentages of primates decline (Reed and Fleagle 1995). Historical circumstances in Africa have no doubt dictated which taxa are found with particular vegetation types, and on other continents a different ancestral stock may have radiated into these niches. For reconstructing ancient vegetation, ecological adaptations are perhaps more easily used than taxonomic groupings.

Makapansgat Methods

The Makapansgat Valley is located in Northern Province, South Africa. The fossil assemblages discussed here derive from the Limeworks Cave. Breccia from the Limeworks has been mined for fossils since 1945 and over 50,000 mammalian specimens have been recovered. Collection assemblages have been designated as Members 1–5 with Member 1 being from the oldest basal travertine and Member 5 being Pleistocene in age. Previous research has determined that the Member 3 assemblage (?3.1–2.9 m.y.) was accumulated by hyenas and porcupines (Maguire et al. 1980; Reed 1996), while the assemblage in Member 4 (?3.0–2.8 m.y.) was likely created by leopards (Maguire et al. 1980) and large birds of prey (Reed 1996). Predators often prey upon particular animals (Brain 1981) and assemblages will reflect only a biased sample of a living community if abundances of specimens are used to reconstruct environments or examine community structure. However, Behrensmeyer (1991) has noted that paleoenvironmental reconstructions based on the presence of taxa can be accurate despite these taphonomic problems. Therefore, I combine analyses of trophic and locomotor-related morphology of all taxa within each large mammalian community with ecological diversity analysis to reconstruct the paleovegetation of these fossil assemblages, as well as to examine the structure of each community.

Sorting, Identification, and Measurement

The mammalian fossils from Makapansgat were collected and prepared by a variety of researchers over about 50 years. Most of the fossil material is stored at the Bernard Price Institute (BPI), University of the Witwatersrand, South Africa. Hominid fossils and many of the

cercopithecine fossils are stored in the Department of Anatomy and Human Biology of the same university. I sorted 6113 craniodontal specimens by matching unidentified isolated teeth, jaw fragments, and skull pieces with fossil taxa that were previously identified or with extant comparative taxa if no fossil taxon matched the specimens.

All measurements were taken with digital calipers and recorded directly into the computer. Allocation of fossil material to ecological categories was based on methodology developed by a number of other researchers. Depending on the mammalian order, different measurements were taken for each taxon.

Indices created by Van Valkenburgh (1988) allowed differentiation of carnivores into meat eaters, meat/bone eaters, and meat/invertebrate eaters. Four of these indices were used in this study: (1) upper canine shape; (2) premolar shape of the largest premolar (the largest premolar defined by area; P_4 for all but hyenas in which P_3 is the largest); (3) relative premolar size; and (4) relative blade length of the lower carnassial, M_1 . Postcranial assignments for carnivores were based on the work of Lewis (1995).

Two methods were used to classify trophic preference of herbivores. First, hypsodonty indices (HI) derived by Janis (1988) were calculated by taking the M_3 height and dividing it by the M_3 width. Height measurements were taken on unworn teeth and width measurements taken at the occlusal surface. In general, mammals in the grazer category have the highest, or most hypsodont, teeth (mean = 5.18) while omnivores have the lowest (mean = 1.16) (Janis 1988). Because Janis discovered that habitat preference affected HI, cranial indices devised by Spencer (1995) were also used to reconstruct the trophic preference of bovids more accurately.

Spencer showed that the ratio of the depth of the mandible at M_2/M_3 to total upper molar row length could separate grazing, mixed feeding (with monocot or dicot preferences), and browsing bovids. This was also the case with the ratio of upper premolar row length to upper molar row length, and palatal width to upper molar row length. As many of these indices as possible were used to predict the

trophic preference of the fossil bovids (Reed 1996). The collection contains many specimens of each species, and often the means of these indices could be used for trophic analysis, rather than predicting trophic behavior through only one specimen. All ungulates were assigned to terrestrial locomotion.

Benefit and McCrossin (1990) have published data on the trophic adaptation of southern African papionins, based on shearing crests (measurements devised by Kay [1984]) and wear pattern. Thus, trophic adaptations for these fossil monkeys were taken from their data when possible. Locomotor assignments for primates were based on the work of Fleagle (Bown et al. 1982) and Ciochon (1993).

Some of the fossil animals, such as the aardvark (*Orycteropus* cf. *O. afer*), were assigned trophic and/or locomotor adaptations based on similarity to their modern congeners. Because aardvark teeth are unique, it is likely that they were used for the same function by living and fossil species. In addition, the humerus of the fossil aardvark exhibited morphology that was indicative of digging. Unfortunately, until morphological comparative samples are available for all extant trophic groups, taxonomic analogy and qualitative morphological comparisons must occasionally be used.

Thus, each fossil mammal was assigned a locomotor and trophic category based on craniodontal and limb morphology. The percentages of each adaptation in the faunas of Members 3 and 4 were calculated. Proportions of adaptations from Makapansgat were then compared with those from extant communities. The fossil assemblages were assigned to a vegetation category using discriminant function analyses (DFA) of both adaptations and taxonomic groups.

Results of Makapansgat Study

Comparison of Adaptations with Extant Communities

Locomotor Adaptations.—The arboreal percentages at Makapansgat place the fossil assemblages within bushland regions (Table 2, Appendix 1). Members 3 (3.5%) and 4 (3.0%) have fairly low percentages of aquatic mam-

mals, about the same as the extant Serengeti Bushland (4.7%), Tarangire National Park (2.1%), and Amboseli National Park (4.35%), which have seasonally flooding rivers. Thus, the presence of the hippopotamus and otter in Member 3 indicates there was a source of water, at least seasonally. The cane rat from Member 4 attests to the presence of water and reed beds at the time that member was accumulated.

Trophic Adaptations.—A high percentage of mammals exhibiting a trophic adaptation to fruit, either alone or in combination with leaves (herbs) and/or insects, indicates an area with rainfall averaging about 810 mm per year and bush or tree cover that is fairly dense (30% to 45% of total ground cover). Member 3 (19.3%) and Member 4 (24.2%) are within the closed woodland/bushland ranges.

Members 3 and 4 contain 3.5% and 6.1% meat/bone eating mammals respectively, as is the case with most nonforested vegetation types. Percentages of fresh-grass grazing animals indicate the presence of edaphic grasslands. Member 3 contains 3.5% and Member 4 contains 3.0% fresh-grass grazing mammals, showing that although these mammals were present, the edaphic grasslands that support this type of mammal may not have been substantial. The percentages of grazing animals (Member 3 = 15.8%; Member 4 = 9.1%) at Makapansgat are at open woodland levels for Member 3 and closed woodland/bushland levels for Member 4 (Table 2).

Plotting the Makapansgat assemblage adaptations with extant vegetation types shows that both fossil sites fall with the bushland/woodland vegetation types (Fig. 1), and the assemblages have few aquatic or fresh-grass grazing adaptations (Fig. 2). Because I only looked at the adaptations that were significantly different among vegetation types, these bivariate plots work well to predict vegetation type in these fossil assemblages accurately.

I also created histograms comparing percentages of adaptations found in Makapansgat Members 3 and 4 with mean percentages of adaptations in extant bushlands and woodlands (Fig. 3). While similar to extant profiles, Makapan 3 differs from both woodland and bushland in that percentages of browsing and

root/bulb eating mammals are much greater, and the percentages of meat/invertebrate eating, omnivory, mixed feeding, and fruit/insect eating are much less. For the meat/invertebrate, omnivory, and fruit/insect eating categories, these reductions are likely due to a bias against these animals. Most extant mammals in these categories are of small-to-medium body size. Thus, they probably have been either completely consumed or not taken as prey by the accumulator of this assemblage, a fossil taxon similar to the striped hyena (Reed 1996). The root/bulb eating animals at Makapansgat are all species of porcupines. Thus, Makapansgat differs ecologically from any extant community because there are higher percentages of root/bulb eating animals, and taxonomically because three hystricomorph rodents exist in the same community. Makapansgat Member 3 is closer to woodland values in grazing, while closer to bushland means in other categories.

Figure 3 shows that Member 4 is also similar in trophic and locomotor percentages, and thus vegetation, to the bushland mean profile. Differences between this fossil assemblage and extant bushlands include high relative percentages of browsing, mixed feeding, fruit/leaf eating, and root/bulb eating mammals and low relative percentages of meat-eating, fruit/insect eating, insectivory, and omnivory. Again, the lack of these latter adaptations could be due to taphonomic biases. This member was accumulated by large birds of prey and leopards. They appear to have preferred medium-sized animals, mostly primates, as is the case with these predators in extant communities (Reed 1996). The high percentage of fruit/leaf eating animals could be the result of low species sample size because larger species are absent. In the grazing category, Member 4 is more like a bushland.

Therefore, the Makapansgat Member 3 assemblage was likely accumulated when the vegetation was bushland-dominated, with limited edaphic grasslands, and riparian woodland. This is much like the Serengeti National Park. The reconstructed vegetation type of Makapansgat Member 4 is perhaps more like a closed woodland/bushland transition, with more riparian woodland.

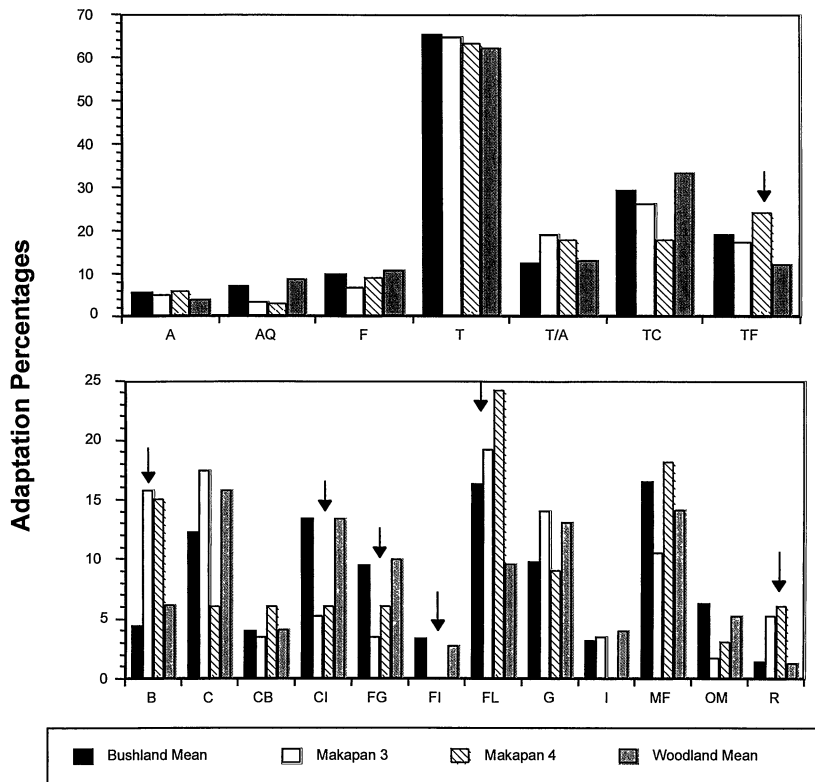


FIGURE 3. Histograms comparing Makapansgat fossil assemblages with means for bushland and woodland habitats. Arrows indicate adaptations in which the fossil assemblages differ from extant bushlands and woodlands. See Appendix 2 for adaptation codes; TC = total carnivory; TF = total frugivory.

Discriminant Function Analysis

Two DF analyses were conducted with Makapansgat Members 3 and 4 entered with no vegetation type so that they could be classified as one of the extant vegetation types. The first DF was performed on arcsine transformations of percentages of taxonomic groups, and the second DF on arcsine transformations of ecological adaptations.

The DFA using the taxonomic groupings could not use five groups that are either no longer extant or present in Africa: Chalicotheriidae, Boselaphini, Ovivovini, Gomphotheriidae, and Machairodontinae. These had to be coded 0 for the extant localities and there was then not enough variation in these groupings for them to be considered in the analysis. Thus, the placement of the Makapansgat members into vegetation types were based on similarities to extant taxa only. The vegetation classification for Makapansgat members is based on the probability of belonging to a par-

ticular vegetation type using the smallest squared Mahalanobis distance from the centroid of that type. Makapansgat Member 3 is classified as closed woodland (100% probability), but the Mahalanobis squared distance from the closed woodland centroid is 1844. Makapansgat Member 4 is classified as bushland (100% probability), but the Mahalanobis squared distance from the closed woodland centroid is 1732. The other distances from the centroid in each vegetation category range from 0.673 to 13. Thus, although the DF *must* classify the fossil sites, they are not near the centroid of any vegetation type. This is likely due to two factors: the missing taxonomic groups and major differences in the distributions of the fossil taxa. For example, most of the Makapansgat fossil primates are papionins, whereas in extant communities there are low percentages of this tribe in all vegetation types.

In the second DFA, using ecological adap-

tations, all of the mammals from the fossil sites could be used as they were assigned ecological adaptations. However, because of the taphonomic biases against meat/invertebrate eating and fruit/insect eating (Reed 1996), these categories were collapsed into Total Carnivory and Total Frugivory for the DFA. Again, classification of vegetation types for the Makapansgat members are based on the probability of belonging to a vegetation type. Member 3 has 100% probability of being a shrubland. The Mahalanobis squared distances from the centroid is 10.87. Member 4 has 99.6% probability of being classified as bushland and 4% as open woodland. The Mahalanobis distance squared from the bushland centroid is 23, while the distance from the open woodland is 34. These distances are closer to the centroids of the extant vegetation types than are those of the taxonomic groupings, but they are still outside of the ranges of extant localities to centroids. Thus, using two methods of discriminant function provided two different vegetation classifications for the fossil assemblages, although in each analysis all extant communities were correctly classified.

Discussion of Makapansgat Paleoeology

Univariate and bivariate analysis of the Makapansgat mammalian adaptations indicate bushland vegetation with probable edaphic grasslands and riparian woodlands. This reconstruction is similar to that based on pollen (Cadman and Rayner 1989) and geological analysis (Rayner et al. 1993). The discriminant functions, however, did not consistently classify these assemblages into bushlands. The Makapansgat assemblages are apparently different enough from extant, mammalian community structure to be assigned only to the closest vegetation type. In the case of Member 3, the closest vegetation types range from closed woodland to shrubland. The Member 4 assemblages were deposited when the vegetation was either bushland or woodland.

In the Makapansgat assemblages, there are higher percentages of giraffids and hystricids than in any extant vegetation type, and other taxa are not represented because of the extinct

taxonomic groups. This alters the representations in the remaining groups. In addition, although the total percentages of primates at Makapansgat are equivalent to those of closed woodlands, the tribal representation is different from any extant community. Thus, results of the DFA analysis, based on taxonomic groupings, suggest that the taxonomic community structures of these Pliocene localities represent a unique pattern.

The taphonomic history of these assemblages likely altered some of the representation of individual species. For example, *Redunca darti* is the most abundant bovid from Member 3, which likely indicates a preference for that taxon by hyenas. The lack of more aquatic animals from this cave site probably indicates that hyenas did not hunt or scavenge much near the river. Studies of modern death assemblages showed that carnivore-accumulated assemblages can be depauperate in both aquatic and arboreal animals (Reed 1996). The Member 4 assemblage contains a preponderance of primate specimens (60%) caused by the accumulating agents, leopards and large birds of prey (Reed 1996). This may give a greater relative percentage of fruit-eating species since other trophic types, such as larger carnivores, may be missing from the assemblage.

Both members, however, differ from extant bushland and woodland communities in their percentages of browsing, mixed feeding, and root/bulb eating. Member 3 also differs in the percentage of grazing mammals. These variances do not seem to be a result of any of the taphonomic processes mentioned earlier. These percentages may represent actual differences between these middle Pliocene and extant communities.

Was this difference only in mammalian community structure, or was there a different vegetation type than is recognized in Africa today? That is, were there vegetation types inhabited by mammals in the Pliocene for which there are no modern analogs? Like animals, various plant species have of course gone extinct and been replaced by others. However, trees, bushes and shrubs have existed for millions of years. Ancient vegetation was contingent on temperature, rainfall, and evapotranspiration. Adaptations of herbivorous animals,

at least, were probably dependent upon ancient vegetation, as they are in extant communities. It is possible that there are mammalian (or other animal) ecological equivalents in extant and extinct vegetation types.

If overall vegetation types were similar over time, then why are percentages of browsing, mixed feeding, grazing, and root/bulb eating different at the time of the Makapansgat deposits? It is conceivable that the structure of both vegetation and mammalian communities has shifted over time. A particular mammalian adaptation may be more prominent in past vegetation types because that particular adaptation reflects a heavy reliance on a particular plant type that is no longer important in extant communities. There are three root/bulb eating species in the Makapansgat assemblages, while only one exists in extant communities. Browsing animals at Makapansgat include two giraffids, a chalicothere, and several bovids that are all extinct species today. It is possible these particular lineages died out randomly. It is also possible intermediate, Pliocene vegetation, i.e., between closed and open woodland, was somehow more productive or nutrient-rich than any extant African vegetation counterpart, and thus supported greater numbers of herbivorous species. This is an area where further study should be interesting.

Conclusions

This study of extant mammalian communities has provided a database of trophic and locomotor adaptations with which to compare African fossil assemblages for patterns of community structure and to reconstruct vegetation types. Mammalian communities have predictable percentages of species with different locomotor and trophic adaptations dependent on vegetation type. For example, arboreal locomotion in forests ranges from 25% to 45% of species present, while in open woodland, this adaptation is found in only 2–5% of the species. Therefore, percentages of various adaptations in mammalian fossil assemblages can be used to predict probable vegetation types under which assemblages were deposited. The ecological patterns seen in these communities can be contrasted with phylo-

genetic patterns to develop a better understanding of evolutionary paleoecology.

Despite the fact that Makapansgat Member 3 was accumulated by hyenas and porcupines, and Member 4 by leopards and large birds of prey, an accurate reconstruction of vegetation type is possible. However, community structure differences between the Makapansgat assemblages and extant communities are apparent, and lead to more questions about ecosystems through time. For example, why are there more browsers in these extinct Pliocene assemblages? Why have primates shifted in tribal representation and in numbers over the past three million years? Further study into these differences may reveal interesting context for mammalian evolutionary histories.

Assemblages of Pliocene fossils, as ecological communities, can be compared across time and African geographic regions without regard to their taxonomic identity. These ecological communities show patterns of organization that change over time. Fossil assemblages, as taxonomic communities, can be compared within these ecological patterns, so that the evolutionary history of various lineages can be studied with regard to ecological adaptations and environmental fluctuations.

Acknowledgments

I thank B. Rubidge (Bernard Price Institute for Palaeontology) and P. V. Tobias (University of the Witwatersrand) for permission to study the Makapansgat fossils. J. Kitching and R. Rayner are appreciated for their help during my stay in South Africa. E. Vrba had sorted much of the Makapansgat bovid material for which I am more than grateful. Thanks to J. Fleagle, C. Janson, C. Marean, F. Grine, and R. Klein for their support during this research. C. Lockwood and J. Kappelman assisted in my understanding of DFA. J. Fleagle, E. Meikle, and L. Spencer read an earlier draft of this paper, P. Andrews, M. Fortelius, and S. Wing also made valuable suggestions, and I thank them all profusely. Thanks to J. Fleagle, who read a final draft and, as usual, made important comments. Thanks also to Tefera. This research was supported by the National Science Foundation, the Leakey Foundation, and the American Association of University Women.

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Appendix 1. Adaptation percentages of extant and extinct communities.

Locality	Rain	DF	Vegetation	A	AQ	F	T	TA	TC	TF	B	C	CB	CI	FG	FI	FL	G	I	MF	OM	R
E of Niger	1596	1	Forest	27.3	15.2	9.1	36.4	12.1	9.1	36.4	3.0	9.1	0.0	0.0	9.1	6.1	30.3	0.0	12.1	15.2	12.1	3.0
Congo Basin	1800	1	Forest	26.4	13.2	9.4	28.3	22.6	26.4	43.4	3.8	15.1	0.0	11.3	1.9	5.7	37.7	0.0	5.7	7.5	7.5	3.8
Kynsna	1016	1	Forest	23.5	5.9	11.8	35.3	23.5	29.4	41.2	0.0	11.8	0.0	17.6	0.0	11.8	29.4	0.0	0.0	5.9	11.8	11.8
Kilimanjaro	1050	1	Forest	31.6	0.0	0.0	63.2	5.3	10.5	42.1	15.8	10.5	0.0	0.0	0.0	10.5	31.6	0.0	0.0	15.8	10.5	5.3
W of Niger	1600	1	Forest	37.5	12.5	9.4	28.1	12.5	6.3	40.6	9.4	6.3	0.0	0.0	6.3	15.6	25.0	0.0	6.3	12.5	12.5	6.3
E of Cross	1550	1	Forest	35.0	17.5	10.0	27.0	10.0	15.0	47.5	2.5	12.5	0.0	2.5	5.0	15.0	32.5	0.0	5.0	10.0	10.0	5.0
Makakou	1800	1	Forest	34.1	7.3	2.4	36.6	19.5	12.2	56.1	2.4	9.8	0.0	2.4	7.3	19.5	36.6	0.0	0.0	9.8	7.3	4.9
Rwenzori NP	900	2	Closed Woodland	15.7	9.8	11.8	45.1	17.7	31.4	27.5	2.0	15.7	3.9	11.8	11.8	7.8	19.6	3.9	3.9	9.8	7.8	2.0
Guinea Woodland	1000	2	Closed Woodland	11.9	8.5	10.2	52.5	16.9	32.2	20.3	5.1	18.6	3.4	10.2	11.9	11.9	18.6	5.1	5.1	11.9	6.8	1.7
Natal Woodland	875	2	CW/Bushland Trans	7.5	7.5	10.0	57.5	17.5	35.0	22.5	5.7	13.2	3.8	11.3	9.4	3.8	15.1	9.4	3.8	17.0	5.7	1.9
Lake Mweru	750	2	CW/Bushland Trans	5.7	8.6	5.7	71.4	8.6	28.6	22.9	5.7	11.4	5.7	11.4	14.3	2.9	20.0	11.4	0.0	14.3	2.9	0.0
W Lunga NP	875	3	Bushland	6.8	11.4	9.1	59.1	13.6	31.8	18.2	4.6	11.4	2.3	18.2	6.8	2.3	15.9	11.4	0.0	15.9	9.1	2.3
Serengeti NP	750	3	Bushland	5.3	8.0	10.7	62.7	13.3	29.3	17.3	4.0	12.0	4.0	13.3	6.7	2.7	14.7	10.7	6.7	17.3	6.7	1.3
Serengeti Bush	803	3	Bushland	6.3	4.7	14.1	59.4	15.6	31.3	17.2	4.7	15.6	4.7	10.9	4.7	3.1	14.1	12.5	6.3	17.2	4.7	1.6
Rukwa Valley	700	3	Bushland	5.8	7.7	9.6	63.5	13.5	28.9	19.2	5.8	13.5	3.9	11.5	9.6	3.9	13.5	9.6	3.9	17.3	5.8	1.9
Kafue NP	821	4	Woodland	5.5	10.9	14.5	52.7	16.4	34.5	12.7	5.5	20.0	3.6	10.9	12.7	3.6	9.1	10.9	5.5	9.1	7.3	1.8
Kruger NP	675	4	Woodland	3.2	7.9	12.7	61.9	14.3	34.9	12.7	7.9	14.3	4.8	15.9	6.3	3.2	9.5	12.7	4.8	14.3	4.8	1.6
Linyanti Swamp	650	4	Woodland	2.9	14.3	2.9	68.6	11.4	28.6	11.4	5.7	11.4	2.9	14.3	17.1	2.9	8.6	17.1	0.0	17.1	2.9	0.0
SS Woodland	650	4	Woodland	4.8	6.0	12.0	66.3	10.8	30.1	13.3	6.0	12.0	3.6	14.5	6.0	2.4	10.8	16.9	6.0	16.9	3.6	1.2
Sudan	689	4	Woodland	3.9	5.9	13.7	62.7	13.7	39.2	11.8	5.9	21.6	5.9	11.8	7.8	2.0	9.8	7.8	3.9	13.7	7.8	2.0
SW Arid	400	5	Shrubland	1.7	6.7	18.3	61.7	11.7	33.3	8.3	6.7	16.7	5.0	11.7	3.3	1.7	6.7	23.3	8.3	13.3	1.7	1.7
Kalahari TV	450	5	Shrubland	0.0	0.0	33.3	60.0	6.7	33.3	6.7	0.0	13.3	6.7	13.3	0.0	0.0	6.7	13.3	20.0	20.0	0.0	6.7
Sahel	450	5	Shrubland/Grassland	0.0	9.7	16.1	51.6	22.6	41.9	6.5	0.0	25.8	3.2	12.9	9.7	0.0	6.5	6.5	6.5	16.1	9.7	3.2
Chobe	650	5	Shrubland	1.8	8.9	17.9	57.1	14.3	28.6	7.1	7.1	14.3	3.6	10.7	10.7	1.8	5.4	16.1	8.9	14.3	5.4	1.8
Amboosi NP	510	5	Shrubland	2.2	4.3	15.2	60.9	17.4	23.9	8.7	10.9	15.2	4.3	8.7	6.5	2.2	6.5	15.2	6.5	15.2	6.5	2.2
Tarangire NP	600	5	Shrubland	2.1	2.1	16.7	68.8	10.4	27.1	8.3	10.4	12.5	6.3	8.3	4.2	0.0	8.3	12.5	10.4	16.7	8.3	2.1
Okavango	600	5	Shrubland	1.9	11.1	18.5	53.7	14.8	33.3	7.4	5.6	14.8	3.7	14.8	9.3	1.9	5.6	16.7	9.3	11.1	5.6	1.9
Kafue Flats	821	6	Grassland	0.0	13.5	2.7	70.3	13.5	37.8	5.4	5.4	21.6	5.4	10.8	16.2	0.0	5.4	16.2	0.0	13.5	5.4	0.0
Serengeti Plains	500	6	Grassland	0.0	0.0	15.8	84.2	0.0	31.6	0.0	0.0	15.8	15.8	0.0	0.0	0.0	0.0	26.3	10.5	21.1	10.5	0.0
SS Grassland	500	6	Grassland	0.0	9.8	17.1	58.5	14.6	36.6	4.9	2.4	17.1	4.9	17.1	2.4	0.0	4.9	24.4	9.8	14.6	0.0	2.4
Namib Desert	125		Desert	0.0	0.0	22.2	50.0	27.8	50.0	11.1	0.0	27.8	11.1	16.7	0.0	0.0	11.1	11.1	5.6	11.1	0.0	5.6
Makapansgat 3				5.3	3.5	7.0	64.6	19.3	26.3	19.3	15.8	17.5	3.5	5.3	5.3	0.0	17.5	15.8	3.5	8.8	1.8	5.3
Makapansgat 4				6.1	3.0	9.1	63.6	18.2	18.2	24.2	12.1	6.1	6.1	6.1	9.1	0.0	24.2	9.1	0.0	18.2	3.0	6.1

Abbreviations: A = arboreal; AQ = aquatic; F = fossorial; TA = terrestrial; TC (total carnivory) = meat, meat/bone, meat/invertebrates; TF (total frugivory) = fruit, fruit/insects, fruit/leaves; B = browse; C = meat; CB = meat/bone; CI = meat/invertebrates; FG = fresh grass; FI = fruit/insects; G = grass; I = insects; OM = omnivorous; R = roots/bulbs.

Appendix 2

Trophic and locomotor adaptations for extant African taxa.

	Loco- motor	Trophic
Artiodactyla		
Bovidae		
Aepycerotini		
<i>Aepyceros melampus</i>	T	MF
Alcelaphini		
<i>Alcelaphus buscelaphus</i>	T	G
<i>Alcelaphus lichtensteini</i>	T	G
<i>Connochaetes gnu</i>	T	MF
<i>Connochaetes taurinus</i>	T	G
<i>Damaliscus dorcus</i>	T	G
<i>Damaliscus lunatus</i>	T	G
Antelopini		
<i>Antidorcas marsupialis</i>	T	MF
<i>Gazella dama</i>	T	MF
<i>Gazella dorcas</i>	T	B
<i>Gazella granti</i>	T	MF
<i>Gazella rufifrons</i>	T	B
<i>Gazella thomsonii</i>	T	MF
Bovini		
<i>Syncerus caffer</i>	T	MF
Cephalophini		
<i>Cephalophus callipygus</i>	T	FL
<i>Cephalophus dorsalis</i>	T	FL
<i>Cephalophus leucogaster</i>	T	FL
<i>Cephalophus maxwelli</i>	T	FL
<i>Cephalophus monticola</i>	T	FL
<i>Cephalophus natalensis</i>	T	FL
<i>Cephalophus niger</i>	T	FL
<i>Cephalophus nigrifrons</i>	T	FL
<i>Cephalophus ogilbyi</i>	T	FL
<i>Cephalophus rufilatus</i>	T	FL
<i>Cephalophus spadix</i>	T	FL
<i>Cephalophus sylvicultor</i>	T	FL
<i>Sylvicapra grimmia</i>	T	FL
Hippotragini		
<i>Hippotragus equinus</i>	T	G
<i>Hippotragus niger</i>	T	MF
<i>Oryx gazella</i>	T	G
Neotragini		
<i>Madoqua kirkii</i>	T	FL
<i>Neotragus batesi</i>	T	B
<i>Neotragus moschatus</i>	T	FL
<i>Oreotragus oreotragus</i>	T	B
<i>Ourebia ourebi</i>	T	MF
<i>Raphicerus campestris</i>	T	B
<i>Raphicerus melanotis</i>	T	B
<i>Raphicerus sharpei</i>	T	MF
Peleinae		
<i>Pelea capreolus</i>	T	MF
Reduncini		
<i>Kobus vardonii</i>	T	FG
<i>Kobus defassa</i>	T	FG
<i>Kobus ellipsiprymnus</i>	T	FG
<i>Kobus kob</i>	T	FG
<i>Kobus leche</i>	T	FG
<i>Redunca arundinum</i>	T	FG
<i>Redunca fulvorufula</i>	T	G
<i>Redunca redunca</i>	T	FG

Appendix 2. Continued.

	Loco- motor	Trophic
Tragelaphini		
<i>Taurotragus derbianus</i>	T	B
<i>Taurotragus eryceros</i>	T	B
<i>Taurotragus oryx</i>	T	MF
<i>Tragelaphus angasi</i>	T	MF
<i>Tragelaphus imberbis</i>	T	B
<i>Tragelaphus scriptus</i>	T	B
<i>Tragelaphus spekei</i>	AQ	MF
<i>Tragelaphus strepsiceros</i>	T	B
Giraffidae		
<i>Giraffa camelopardalis</i>	T	B
Hippopotimidae		
<i>Choeropsis liberiensis</i>	AQ	FG
<i>Hippopotamus amphibius</i>	AQ	FG
Suidae		
<i>Hylochoerus meinertzhageni</i>	T	MF
<i>Phacochoerus aethiopicus</i>	T	G
<i>Potamochoerus porcus</i>	T	OM
Tragulidae		
<i>Hyemoschus aquaticus</i>	T	FG
Carnivora		
Canidae		
<i>Canis adustus</i>	T	CI
<i>Canis aureus</i>	T	OM
<i>Canis mesomelas</i>	T	CI
<i>Lycaon pictus</i>	T	CB
<i>Otocyon megalotis</i>	T	I
<i>Vulpes chama</i>	T	C
<i>Vulpes pallida</i>	T	C
Felidae		
<i>Acinonyx jubatus</i>	T	C
<i>Felis aurata</i>	TA	C
<i>Felis caracal</i>	TA	C
<i>Felis libyca</i>	TA	C
<i>Felis nigripes</i>	TA	C
<i>Felis serval</i>	TA	C
<i>Panthera leo</i>	T	C
<i>Panthera pardus</i>	TA	C
Herspestidae		
<i>Helogale parvula</i>	F	CI
<i>Herpestes ichneumon</i>	T	CI
<i>Herpestes naso</i>	T	CI
<i>Herpestes pulverulentus</i>	T	CI
<i>Herpestes sanguineus</i>	T	CI
<i>Ichneumia albicauda</i>	T	CI
<i>Mungos gambianus</i>	T	CI
<i>Mungos mungo</i>	F	CI
<i>Paracynictis selousi</i>	T	C
<i>Rhynchogale melleri</i>	T	CI
<i>Suricata suricatta</i>	F	CI
Hyaenidae		
<i>Crocuta crocuta</i>	T	CB
<i>Hyaena brunea</i>	T	CB
<i>Hyaena hyaena</i>	T	CB
<i>Proteles cristatus</i>	T	I
Mustelidae		
<i>Aonyx capensis</i>	AQ	CI
<i>Aonyx congica</i>	AQ	CI
<i>Ictonyx straitus</i>	F	CI

Appendix 2. Continued.

	Loco-motor	Trophic
<i>Lutra maculicollis</i>	AQ	C
<i>Mellivora capensis</i>	F	OM
<i>Poecilictis libyca</i>	T	C
<i>Poecilogale albinucha</i>	T	C
Viverridae		
<i>Atilax paludinosus</i>	AQ	C
<i>Bdeogale crassicauda</i>	T	CI
<i>Bdeogale nigripes</i>	T	C
<i>Crossarchus obscurus</i>	T	I
<i>Cynictis penicillata</i>	F	I
<i>Genetta felina</i>	TA	C
<i>Genetta genetta</i>	TA	CI
<i>Genetta pardina</i>	T	C
<i>Genetta poensis</i>	TA	C
<i>Genetta servilina</i>	TA	C
<i>Genetta thierryi</i>	T	CI
<i>Genetta tigrina</i>	TA	CI
<i>Genetta victoriae</i>	A	C
<i>Nandinia binotata</i>	A	OM
<i>Viverra civetta</i>	T	OM
Hyracoidea		
Procaviidae		
<i>Dendrohyrax arboreus</i>	A	B
<i>Dendrohyrax dorsalis</i>	TA	FL
<i>Heterohyrax brucei</i>	T	MF
<i>Procavia capensis</i>	T	MF
<i>Procavia ruficeps</i>	T	FL
Insectivora		
Erinaceidae		
<i>Atelerix frontalis</i>	T	OM
<i>Erinaceus albiventris</i>	T	I
Tenrecidae		
<i>Potomogale velox</i>	AQ	CI
Lagomorpha		
Leporidae		
<i>Bunolagus monticularis</i>	T	B
<i>Lepus capensis</i>	T	MF
<i>Lepus crawshayi</i>	T	MF
<i>Lepus saxafilis</i>	T	G
<i>Pronolagus crassicaudatus</i>	T	G
<i>Pronolagus randensis</i>	T	G
<i>Pronolagus rupestris</i>	T	G
Perissodactyla		
Equidae		
<i>Equus burchelli</i>	T	G
<i>Equus zebra</i>	T	G
Rhinocerotidae		
<i>Ceratotherium simum</i>	T	G
<i>Diceros bicornus</i>	T	B
Pholidota		
Manidae		
<i>Manis gigantea</i>	F	I
<i>Manis temminckii</i>	F	I
<i>Manis tetradactyla</i>	F	I
<i>Manis tricuspis</i>	A	I
Primates		
Cercopithecidae		
Cercopithecini		
<i>Allenopithecus nigroviridis</i>	T	FI
<i>Cercopithecus aethiops</i>	TA	FL

Appendix 2. Continued.

	Loco-motor	Trophic
<i>Cercopithecus ascanius</i>	A	FI
<i>Cercopithecus cephus</i>	A	FI
<i>Cercopithecus erythrogaster</i>	A	FL
<i>Cercopithecus erythrotis</i>	A	FL
<i>Cercopithecus mitas</i>	A	FL
<i>Cercopithecus mona</i>	A	FL
<i>Cercopithecus neglectus</i>	A	FL
<i>Cercopithecus nictitans</i>	A	FL
<i>Cercopithecus pogonias</i>	T	FI
<i>Miopithecus talapoin</i>	A	FI
Colobini		
<i>Colobus guereza</i>	A	FL
<i>Colobus polykomos</i>	A	FL
<i>Piliocolobus badius</i>	A	FL
<i>Procolobus verus</i>	TA	FL
Papionini		
<i>Cercocebus albigena</i>	A	FL
<i>Cercocebus aterrimus</i>	A	FL
<i>Cercocebus galeritus</i>	TA	FL
<i>Cercocebus torquata</i>	A	FL
<i>Erythrocebus patas</i>	T	FL
<i>Mandrillus leucophaeus</i>	TA	FL
<i>Mandrillus sphinx</i>	TA	FL
<i>Papio anubis</i>	TA	FL
<i>Papio cynocephalus</i>	TA	FL
<i>Papio ursinus</i>	TA	FL
Lorisidae		
<i>Arctocebus calabarensis</i>	A	FI
<i>Euoticus elegantulus</i>	A	FI
<i>Galago moholi</i>	A	FI
<i>Galago senegalensis</i>	A	FI
<i>Galagoides alleni</i>	A	FI
<i>Galagoides demidovii</i>	A	FI
<i>Otolemur crassicaudatus</i>	A	FI
<i>Perodicticus potto</i>	A	FI
Pongidae		
<i>Gorilla gorilla</i>	T	FL
<i>Pan paniscus</i>	TA	F
<i>Pan troglodytes</i>	TA	FL
Proboscidea		
Elephantidae		
<i>Loxodonta africana</i>	T	MF
Rodentia		
Hystriidae		
<i>Atherurus africanus</i>	T	R
<i>Hystrix africaeaustralis</i>	F	R
<i>Hystrix cristata</i>	F	R
Muridae		
<i>Cricetomys emini</i>	F	R
<i>Cricetomys gambianus</i>	F	OM
Pedetidae		
<i>Pedetes capensis</i>	F	G
Thryonomidae		
<i>Thryonomys gregorianus</i>	T	FG
<i>Thryonomys swinderianus</i>	T	FG
Tubulidentata		
Orycteropodidae		
<i>Orycteropus afer</i>	F	I

Abbreviations: A = arboreal; AQ = aquatic; F = fossorial; TA = terrestrial/arboreal; T = terrestrial; B = browse; C = meat; CB = meat/bone; CI = meat/invertebrates; FG = fresh grass; FI = fruit/insects; FL = fruit/leaves; G = grass; I = insects; MF = leaves/grass; OM = omnivorous; R = roots/bulbs.

Appendix 3. Taxonomic percentages of extant and extinct communities.

Locality	DF	AEPY	ALCE	ANTEL	BOV	CAN	CEPH	CER	COLO	ELEP	EQU	FEL	GIR	HERP	HIPPO	HYAE	HYRA	HYS	INS	LAG	LORIS
W of Niger	1	0.0	0.0	0.0	3.0	0.0	9.1	9.1	0.0	3.0	0.0	3.0	0.0	6.1	0.0	6.1	3.0	3.0	3.0	3.0	6.1
Congo	1	0.0	0.0	0.0	1.9	0.0	11.3	11.3	3.8	1.9	0.0	5.7	0.0	9.4	0.0	1.9	1.9	1.9	1.9	0.0	3.8
Knysna	1	0.0	0.0	0.0	0.0	0.0	11.8	11.8	0.0	0.0	0.0	5.9	0.0	17.7	0.0	0.0	5.9	5.9	0.0	0.0	11.8
Kilimanjaro	1	0.0	0.0	0.0	5.3	0.0	10.5	5.3	5.3	5.3	0.0	10.5	5.3	0.0	0.0	0.0	5.3	5.3	0.0	0.0	10.5
E of Niger	1	0.0	0.0	0.0	3.1	0.0	6.3	9.4	0.0	3.1	0.0	3.1	0.0	3.1	0.0	6.3	3.1	3.1	0.0	0.0	15.6
Cross	1	0.0	0.0	0.0	2.5	0.0	10.0	7.5	0.0	2.5	0.0	2.5	0.0	7.5	0.0	2.5	2.5	2.5	2.5	0.0	12.5
Makakou	1	0.0	0.0	0.0	2.4	0.0	14.6	9.8	2.4	2.4	0.0	4.9	0.0	0.0	0.0	2.4	2.4	2.4	0.0	0.0	14.6
Rwenzori NP	2	0.0	2.0	0.0	2.0	3.9	7.8	5.9	3.9	2.0	0.0	9.8	0.0	9.8	0.0	2.0	2.0	2.0	0.0	2.0	5.9
Guinea Woodland	2	0.0	1.7	1.7	1.7	5.1	3.4	5.1	5.1	1.7	0.0	8.5	1.7	10.2	1.7	1.7	1.7	1.7	1.7	1.7	1.7
Natal	2	0.0	0.0	0.0	0.0	0.0	5.0	5.0	0.0	0.0	0.0	7.5	0.0	10.0	0.0	5.0	5.0	2.5	0.0	7.5	5.0
Lake Mweru	2	2.9	2.9	0.0	2.9	5.7	5.7	2.9	2.9	2.9	2.9	5.7	0.0	11.4	5.7	2.9	2.9	0.0	0.0	0.0	2.9
W Lunga NP	3	2.3	2.3	0.0	2.3	2.3	6.8	4.5	0.0	2.3	2.3	6.8	0.0	11.4	4.5	2.3	2.3	2.3	0.0	0.0	2.3
Serengeti NP	3	1.3	4.0	2.7	1.3	6.8	5.3	2.7	1.3	1.3	1.3	8.0	1.3	8.0	2.7	1.3	4.0	2.7	1.3	1.3	2.7
Serengeti Bush	3	1.6	4.7	3.1	1.6	6.3	3.1	3.1	1.6	1.6	1.6	9.4	1.6	7.8	1.6	1.6	4.7	3.1	1.6	0.0	3.1
Rukwa Valley	3	1.9	3.9	0.0	1.9	3.9	3.9	3.9	0.0	1.9	1.9	11.5	1.9	9.6	3.9	1.9	1.9	1.9	0.0	1.9	3.9
Kafue NP	4	1.8	3.6	0.0	0.0	3.6	1.8	3.6	0.0	1.8	1.8	10.9	0.0	9.1	3.6	1.8	1.8	1.8	0.0	1.8	3.6
Kruger NP	4	1.6	3.2	0.0	1.6	4.8	3.2	1.6	0.0	1.6	1.6	9.5	1.6	9.5	3.2	1.6	4.8	1.6	0.0	1.6	3.2
Linyanti Swamp	4	2.9	5.7	0.0	2.9	2.9	2.9	2.9	0.0	0.0	2.9	8.6	2.9	5.7	5.7	2.9	2.9	0.0	0.0	2.9	2.9
SS Woodland	4	1.2	4.8	0.0	1.2	6.0	3.6	2.4	0.0	1.2	1.2	7.2	1.2	9.6	3.6	1.2	3.6	1.2	0.0	6.0	2.4
Sudan	4	0.0	3.9	2.0	2.0	7.8	3.9	3.9	0.0	2.0	0.0	11.8	2.0	5.9	2.0	2.0	3.9	2.0	2.0	3.9	2.0
SW Arid	5	1.7	6.8	1.7	0.0	6.8	1.7	1.7	0.0	1.7	3.3	10.0	1.7	10.0	1.7	1.7	5.0	1.7	0.0	8.3	1.7
Kalahari TV	5	0.0	0.0	6.7	0.0	20.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0	13.3	6.7	0.0	6.7	0.0	6.7	0.0	0.0
Sahel	5	0.0	3.2	9.7	0.0	6.5	0.0	3.2	0.0	3.2	0.0	12.9	0.0	6.5	0.0	3.2	3.2	3.2	3.2	3.2	0.0
Chobe NP	5	1.8	3.6	0.0	1.8	7.1	1.8	1.8	0.0	1.8	1.8	10.7	1.8	5.4	5.4	1.8	3.6	0.0	1.8	0.0	1.8
Amboseli NP	5	2.2	4.4	6.5	2.2	6.5	0.0	2.2	0.0	2.2	2.2	13.0	2.2	4.4	2.2	2.2	6.5	0.0	2.2	2.2	2.2
Tarangire NP	5	2.1	4.2	4.2	2.1	6.3	2.1	2.1	0.0	0.0	2.1	8.3	2.1	6.3	4.2	0.0	4.2	2.1	0.0	2.1	0.0
Okavango	5	1.9	3.7	0.0	1.9	7.4	1.9	1.9	0.0	1.9	1.9	11.1	1.9	9.3	5.6	1.9	3.7	0.0	1.9	0.0	1.9
Kafue Flats	6	2.7	5.4	0.0	2.7	5.4	2.7	0.0	0.0	2.7	2.7	13.5	0.0	5.4	5.4	2.7	2.7	0.0	0.0	0.0	0.0
Serengeti Plains	6	0.0	10.5	10.5	0.0	21.1	0.0	0.0	0.0	0.0	5.3	10.5	0.0	0.0	5.3	0.0	10.5	0.0	0.0	5.3	0.0
SS Grassland	6	0.0	7.3	2.4	0.0	4.9	2.4	0.0	0.0	0.0	2.4	12.2	0.0	12.2	0.0	2.4	7.3	2.4	0.0	9.8	0.0
Makapansgat 3		3.5	5.3	3.5	1.8	5.3	1.8	0.0	3.5	0.0	1.8	12.3	3.5	1.8	1.8	1.8	3.5	1.8	5.3	0.0	1.8
Makapansgat 4		0.0	3.0	3.0	3.0	6.1	0.0	0.0	3.0	0.0	0.0	3.0	3.0	3.0	0.0	0.0	6.1	9.1	6.1	0.0	0.0

Appendix 3. Continued.

Locality	MAN	MUR	MUST	NEO	PAPI	PED	PEL	PONG	RED	RHINO	SUID	THRY	TRAG	TRAGU	TUB	VIV	MACH	BOS	OVI	CHAL	COMP	HOM
W of Niger	6.1	6.1	0.0	0.0	3.0	0.0	0.0	3.0	0.0	0.0	3.0	3.0	6.1	3.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.0
Congo	3.8	1.9	5.7	0.0	5.7	0.0	0.0	5.7	0.0	0.0	1.9	0.0	5.7	1.9	1.9	9.4	0.0	0.0	0.0	0.0	0.0	0.0
Knyсна	0.0	5.9	0.0	0.0	5.9	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0	0.0	11.8	0.0	0.0	0.0	0.0	0.0	0.0
Kilimanjaro	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	5.3	5.3	0.0	10.5	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0
E of Niger	3.1	6.3	0.0	3.1	3.1	0.0	0.0	3.1	0.0	0.0	3.1	3.1	6.3	3.1	0.0	9.4	0.0	0.0	0.0	0.0	0.0	0.0
Cross	2.5	5.0	2.5	0.0	7.5	0.0	0.0	5.0	0.0	0.0	2.5	2.5	5.0	2.5	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0
Makakou	0.0	2.4	0.0	0.0	7.3	0.0	0.0	4.9	2.4	0.0	4.9	0.0	4.9	2.4	0.0	12.2	0.0	0.0	0.0	0.0	0.0	0.0
Rwenzori NP	2.0	0.0	5.9	0.0	2.0	0.0	0.0	2.0	5.9	0.0	5.9	2.0	3.9	0.0	2.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0
Guinea Woodland	1.7	1.7	5.1	3.4	3.4	0.0	0.0	0.0	6.8	1.7	5.1	1.7	3.4	0.0	1.7	5.1	0.0	0.0	0.0	0.0	0.0	0.0
Natal	0.0	0.0	7.5	10.0	2.5	0.0	2.5	0.0	7.5	0.0	2.5	2.5	2.5	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0
Lake Mweru	0.0	0.0	0.0	5.7	2.9	0.0	0.0	0.0	8.6	2.9	5.7	0.0	8.6	0.0	0.0	2.9	0.0	0.0	0.0	0.0	0.0	0.0
W Lunga NP	0.0	2.3	6.8	4.5	2.3	0.0	0.0	0.0	6.8	0.0	4.5	0.0	6.8	0.0	0.0	6.8	0.0	0.0	0.0	0.0	0.0	0.0
Serengeti NP	1.3	1.3	5.3	5.3	2.7	0.0	0.0	0.0	4.0	1.3	4.0	1.3	4.0	0.0	1.3	4.0	0.0	0.0	0.0	0.0	0.0	0.0
Serengeti Bush	1.6	0.0	4.7	6.3	3.1	1.6	0.0	0.0	4.7	1.6	3.1	0.0	3.1	0.0	1.6	4.7	0.0	0.0	0.0	0.0	0.0	0.0
Rukwa Valley	1.9	0.0	1.9	5.8	1.9	0.0	0.0	0.0	5.8	0.0	3.9	1.9	7.7	0.0	1.9	3.9	0.0	0.0	0.0	0.0	0.0	0.0
Kafue NP	1.8	1.8	7.3	3.6	1.8	0.0	0.0	0.0	7.3	0.0	3.6	1.8	7.3	0.0	1.8	5.5	0.0	0.0	0.0	0.0	0.0	0.0
Kruger NP	1.6	0.0	6.4	4.8	1.6	1.6	1.6	0.0	4.8	3.2	3.2	1.6	6.4	0.0	1.6	4.8	0.0	0.0	0.0	0.0	0.0	0.0
Linyanti Swamp	0.0	0.0	5.7	2.9	2.9	0.0	0.0	0.0	11.4	0.0	2.9	2.9	8.6	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0
SS Woodland	1.2	0.0	4.8	7.2	1.2	0.0	1.2	0.0	6.0	2.4	2.4	0.0	6.0	0.0	1.2	4.8	0.0	0.0	0.0	0.0	0.0	0.0
Sudan	0.0	2.0	9.8	2.0	2.0	0.0	0.0	0.0	5.9	2.0	2.0	0.0	2.0	0.0	2.0	5.9	0.0	0.0	0.0	0.0	0.0	0.0
SW Arid	1.7	0.0	6.8	5.0	1.7	1.7	1.7	0.0	1.7	3.3	1.7	0.0	3.3	0.0	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0
Kalahari TV	0.0	0.0	0.0	6.7	0.0	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	6.7	0.0	0.0	0.0	0.0	0.0	0.0
Sahel	0.0	0.0	16.1	0.0	3.2	0.0	0.0	0.0	6.5	0.0	3.2	0.0	0.0	0.0	3.2	6.5	0.0	0.0	0.0	0.0	0.0	0.0
Chobe NP	1.8	0.0	7.1	3.6	1.8	1.8	0.0	0.0	7.1	3.6	3.6	1.8	7.1	0.0	1.8	3.6	0.0	0.0	0.0	0.0	0.0	0.0
Amboseli NP	0.0	0.0	4.4	4.4	2.2	2.2	0.0	0.0	4.4	2.2	2.2	0.0	6.5	0.0	2.2	4.4	0.0	0.0	0.0	0.0	0.0	0.0
Tarangire NP	6.3	0.0	4.2	6.3	2.1	0.0	0.0	0.0	4.2	2.1	4.2	0.0	8.3	0.0	2.1	4.2	0.0	0.0	0.0	0.0	0.0	0.0
Okavango	1.9	0.0	7.4	1.9	1.9	1.9	0.0	0.0	5.6	1.9	3.7	1.9	5.6	0.0	1.9	3.7	0.0	0.0	0.0	0.0	0.0	0.0
Kafue Flats	0.0	0.0	5.4	5.4	0.0	0.0	0.0	0.0	10.8	0.0	5.4	0.0	10.8	0.0	0.0	8.1	0.0	0.0	0.0	0.0	0.0	0.0
Serengeti Plains	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	5.3	0.0	5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SS Grassland	2.4	0.0	4.9	4.9	2.4	2.4	2.4	0.0	2.4	2.4	0.0	0.0	2.4	0.0	2.4	2.4	0.0	0.0	0.0	0.0	0.0	0.0
Makapansgat 3	1.8	0.0	1.8	3.5	8.8	0.0	0.0	0.0	1.8	3.5	3.5	0.0	5.3	0.0	1.8	0.0	1.8	1.8	1.8	1.8	0.0	1.8
Makapansgat 4	0.0	0.0	0.0	3.0	15.2	0.0	0.0	0.0	3.0	3.0	6.1	3.0	9.1	0.0	0.0	0.0	0.0	0.0	3.0	0.0	3.0	3.0

Abbreviations: DF = discriminant function, AEPY = Aepyrotini, ALCE = Alcelaphini, ANTEL = Antelopini, BOV = Bovini, CAN = Canidae, CEPH = Cephalophini, CERC = Cercopithecini, COLO = Colobinae, ELEP = Elephantidae, EQU = Equidae, FEL = Felinae, GIR = Giraffidae, HERP = Herpestidae, HIP = Hippotragini, HIPPO = Hippopotamidae, HYAEN = Hyainae, HYRA = Hyracoidea, HYS = Hystricidae, INS = Insectivora, LAG = Lagomorpha, LOR = Lorisidae, MAN = Manidae, MUR = Muridae, MUST = Mustelidae, NEO = Neotragini, PAPI = Papionini, PED = Pedetidae, PEL = Peleinae, PONG = Pongidae, RED = Reductini, RHINO = Rhinocerotidae, SUID = Suidae, THRY = Thryonemidae, TRAG = Tragelaphini, TRAGU = Tragulidae, TUB = Tubulidentata, VIV = Viverridae, MACH = Machaerodontinae, BOS = Boselaphini, OVI = Oribovini, CHAL = Chalicotheriidae, COMP = Gomphotheriidae, HOM = Hominae.